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Observations of the reproductive activities of white-tailed ptarmigan (Lagopus leucurus) in Glacier Park Montana

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OBSERVATIONS ON THE REPRODUCTIVE ACTIVITIES OF WHITE-TAILED PTARMIGAN (LAGOPUS LEUCURUS) IN GLACIER PARK, MONTANA

by

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INTRODUCTION

Purpose and Scope

The White-tailed Ptarmigan, Lagopus leucurus, is perhaps the least known member of the grouse family, Tetraonidae, in North America. Very few scientific investigations have been made on this species and only distributional records relating to Montana birds have been published.

Members of the grouse family are noted for their specialized and unique courtship behaviors. It is the purpose of this paper to describe reproductive behavior of the White-tailed Ptarmigan, from spring courtship through independence of the grown chicks in September.

The reproductive activities herein described are those of a group of about one hundred individually marked ptarmigan which resided at least part of the summer in an area near Logan Pass, Glacier National Park, Montana.

Methods

The observations included in this paper were made between June 6, 1959 and October 5, 1959, the period during which the Logan Pass road was accessible to travel. The reproductive cycle probably was represented completely during these four months at Logan Pass, since in 1959 spring, summer, and fall phenological seasons were essentially compressed into this period of time (see Page 12).

Observations on ptarmigan were accomplished through systematic searching of the area to locate birds, then watching with the aid of binoculars. Written records were made on the spot, with as much detail

as time permitted. Further records were made with both still and movie cameras.

Ptarmigan were captured, generally with a long-handled hand net, and measurements and other morphological data were recorded. The birds were then banded with numbered aluminum Fish and Wildlife Service leg-bands, and one or more colored plastic leg bands (A. C. Hughes Company, Hampton Hill, Middlesex, England). In order to allow recognition of individual ptarmigan at a distance, no two birds were color-banded alike. Young birds were banded as near to flight age (ten days) as possible and then color-banded at about the age of independence (seven to eight weeks) in the fall. An attempt was made to recapture all birds at least once per month to record physical changes and insure banding permanence.

THE STUDY AREA

Boundaries

The study area at Logan Pass lies astride the Continental Divide and to the south of the Going-to-the-Sun-Road.

The approximate eastern boundary is a line running south from the highway parking lot to the watershed division between the south and north forks of Reynolds Creek. The southern boundary runs west along this watershed divide to the 7500 foot contour on the east side of the continental divide. The western boundary follows this 7500 foot contour north to Hidden Lake Pass and includes this pass area west to the lake overlook. The western boundary then follows the 7500 foot contour back to the north around the moraines at the foot of Mt. Clements to the northeast shoulder of Mt. Oberlin. The northern boundary is approximately a straight line from this shoulder to the parking lot at Logan Pass. The total area encompasses somewhat over three square miles or about 2000 acres (see map, page 4).

Topography

The study area has a fairly even, bench-like appearance. Glacial levelling probably has been the major contributing factor to this appearance. Elevation ranges from 6400 to 7400 feet on this benchland, generally rising fairly uniformly from northeast to southwest (see Figure 1).

The major drainage system on the study area is the North Fork of Reynolds Creek. This stream has its source in three areas along the Continental Divide on the southwest boundary of the study area.

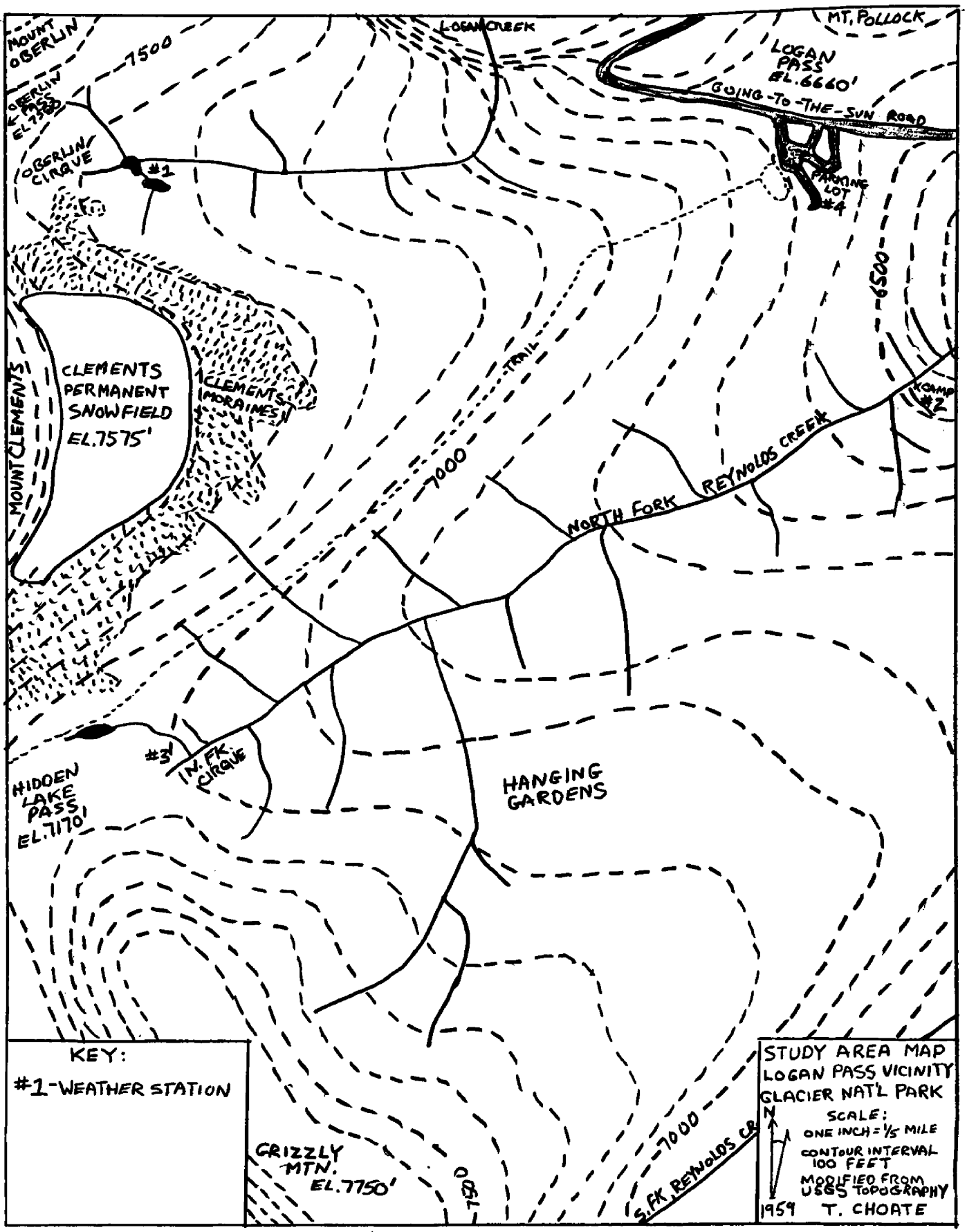

FIGURE 1. Map of Logan Pass and vicinity showing study area

The secondary drainage system on the area is on the northern side of the Continental Divide and originates mainly in the Oberlin Cirque.

The Logan Pass area is characterized by numerous ledges of various widths ranging from a few feet to a hundred yards in width. These ledges resulted from the erosion and exposure of more resistant layers of the Algonkian argyllitic strata which lie at a relatively low angle of dip along the Continental Divide. The wide, well-vegetated ledges in the southern parts of the study area have become known as the "Hanging Gardens." -These and smaller ledges seem to be widely used by ptarmigan, especially early in the season.

The summits around Logan Pass (Mts. Reynolds, Clements, Oberlin, and Pollock) are the last remnants of a very old cirque established in Kansan and Nebraskan periods of Pleistocene Glaciation when ice covered all but the highest ridges of the park. In later glacial periods, particularly the latest or Wisconsin Advance, the ice was shallower and the present valleys of Avalanche, MacDonald, and Reynolds Creeks were excavated well below the level of Logan Pass (Ruhle, 1957).

The actual crest of the Continental Divide and its associated peaks lies for the most part to the west of the study area. Prevailing winds throughout the summer and at least part of the winter are from the west. Therefore at least part of the area is protected from the full velocities of westerly winds. The occurrence of fairly tall timber along the east facing portions of Grizzly Mountain may be attributable to reduced wind velocities. Wind enters the area primarily through Hidden Lake Pass, but Oberlin Pass and Logan Pass are secondary sources.

The topography to the west of the study area serves also to cause considerable rainfall and snow accumulation on the study area and adjacent land. Clouds frequently form as moist wind strikes Mt. Clements. This often causes rain or snow to fall subsequently on the Logan Pass area. Some lessened insolation is caused by the higher elevations to the west and slight northeasterly aspect of the area. This lessened insolation, plus the lessened wind and increased precipitation combine to cause snow accumulation in many parts of the study area. Certainly the recently active Clements Glacier and the presence of several small cirques on or near the study area testify to this effect from the topography.

Weather

Weather records were kept throughout the fourteen weeks from June 19 to September 23 inclusive. During this period, records were made of the daily fluctuations of temperature and relative humidity. Wind velocity was measured two or more times daily and estimated at other times. Cloud cover was estimated at the time the wind measurements were made. Precipitation was measured continuously from August 11 until the end of the study (see Table I).

Weather information was gathered in four locations at Logan Pass. Three of these locations were used as weather stations representative of certain topographic aspects of the study area. The fourth was used only for supplemental information.

The general pattern of gathering data included morning and evening records at Station #2. Mid-day records were usually taken at both the pass and cirque stations (#3 and #1). (See Figure 1.)

The weekly data in Table I are summarized from all stations.

Average daytime measurements are derived from all records taken between 8 A. M. and 5 P. M.

TABLE I. Weekly weather data from Logan Pass stations

1959 Week Period	Temperature (°F) Average Day	Average Max.	Average Min.	Extreme Max.	Extreme Min.	% Relative Humidity Average Day	Average Max.	Average Min.	Extreme Max.	Extreme Min.	Accum. Snow Depth
June 6 June 13	nt					nt					10-20 feet
June 14 June 20	inc 64	76	46	86	45	inc 65	90	52	100	51	6-10 feet
June 21 June 27	46	56	39	70	32	86	98	76	100	50	55 in.
June 28 July 4	46	57	36	69	27	80	95	68	100	62	40 in.
July 5 July 11	49	60	37	75	35	64	92	52	100	45	11 in.
July 12 July 18	61	73	45	79	40	58	72	45	95	28	none
July 19 July 25	70	80	46	87	42	61	74	47	83	42	
July 26 Aug. 1	63	72	39	84	29	59	80	47	100	38	
Aug. 2 Aug. 8	59	66	41	76	33	60	66	54	100	50	
Aug. 9 Aug. 15	50	61	39	71	34	66	78	49	100	44	
Aug. 16 Aug. 22	46	53	39	70	36	79	94	69	100	57	
Aug. 23 Aug. 29	44	49	37	55	27	87	98	82	100	68	
Aug. 30 Sept. 5	inc 44			56	22	85			100	63	
Sept. 6 Sept. 12	46	51	37	76	26	86	92	78	100	54	

TABLE I (continued)

1959 Week Period	Temperature (°F) Average Day	Average Max.	Average Min.	Extreme Max.	Extreme Min.	% Relative Humidity Average Day	Average Max.	Average Min.	Extreme Max.	Extreme Min.	Accum. Snow Depth
Sept. 13 Sept. 19	43	49	35	65	27	93	100	87	100	60	
Sept. 20 Sept. 26	inc 39	43	35	43	33	97	100	96	100	90	3 in.
Sept. 27 Oct. 4	inc 36					nt					13 in.
Avg. June	inc 47	57	38	86	27	inc 80	94	70	100	50	75 in.
Avg. July	61	71	42	87	29	60	80	48	100	28	3 in.
Avg. Aug.	50	57	39	76	27	66	84	63	100	44	
Avg. Sept.	43	48	36	76	22	89	96	80	100	54	2 in.
Avg. Season	50	58	39	87	22	74	88	65	100	28	20 in.

nt - not taken

inc - incomplete records

TABLE II. Weekly weather data from Logan Pass stations (Part 2)

1959 Week Period	Wind Velocity Average M.P.H. Day	Max.	Min.	Extreme Max.	Cloud % Average Day	Week	Precipitation in Inches Avg. Day*	Extreme Max.	Min.	Week Total	Form
6/6	inc				inc		nt			over	
6/13	7				75					1 day	hail
6/14	inc						nt			over	
6/20	4.3	8.2	1.2	25	40	26				1 day	rain
6/21							nt				snow
6/27	3.1	5.4	2.1	10	78	78				6 days	rain
6/28							nt				snow
7/4	4.9	6.6	3.0	25	70	62				4 days	rain
7/5							nt				hail
7/11	5.1	9.1	3.1	17	75	52				3 days	rain
7/12							nt				
7/18	4.1	7.9	1.1	12	10	2				none	
7/19							nt				
7/25	2.7	5.6	.5	11	30	10				none	
7/26							nt				
8/1	3.5	7.8	1.8	21	40	20				1 day	snow
8/2							nt				
8/8	4.7	7.4	2.4	20	40	12				½ day	rain
8/9										.72	fog
8/15	3.0	6.1	1.0	11	67	50	.28	.70	T	2½ days	rain
8/16										3.26	fog
8/22	6.1	8.9	1.8	16	88	85	.64	1.1	T	5 days	rain
8/23										2.53	fog
8/29	4.0	5.9	1.1	10	74	70	.50	1.4	.04	5 days	rain
8/30	inc									3.18	snow
9/5	10	15	5	30?	72	65	.80			4 days	rain
9/6	inc									3.55	snow
9/12				25	80	45	1.0			3½ days	rain
9/13										2.48	snow
9/19	3.1	5.0	1.5	12	95	95	.35	1.1	.07	7 days	rain

TABLE II (continued)

1959 Week Period	Wind Velocity Average M.P.H. Day	Max.	Min.	Extreme Max.	Cloud % Average Day	Week	Precipitation in Inches Avg. Day*	Extreme Max.	Min.	Week Total	Form
9/20	inc									.96	snow
9/26	3.5			11	88	56	.24	.49	.01	4 days	rain
9/27	inc						nt			over	fog
10/4	4			10	75					2 days	snow
Avg. June	inc 4.2	6.9	2.1	25	65	55	nt			3 days	snow rain
Avg. July	3.8	7.6	1.5	21	40	21	nt			1 day	rain
Avg. Aug.	4.3	7.1	1.6	20	67	54	.53	1.4	T	3.3 day	fog rain
Avg. Sept.	5.2	9.5	3.0	30	81	64	.79	1.1	.01	5 days	snow rain
Avg. Season	4.4	7.9	2.0	30	63	48	.66	1.4	T	3.1 day	snow rain

*Days on which precipitation occurred only

The summer of 1959 was phenologically shorter, cooler, and wetter than the previous summer. A preliminary investigation of ptarmigan at Logan Pass in the summer of 1958 by Evans and Fisher showed nesting and other phenologically related occurrences to have taken place approximately two to three weeks earlier. Their records further indicate at any given time a much smaller snow depth than in 1959. In 1958 all major snowfields dried up by the period of maximum heat at the end of July. In contrast, snowfields of considerable extent never melted during the summer of 1959. A record snowdrift, seventy-four feet deep, was measured near Logan Pass on the Going-to-the-Sun Road in early June, 1959, when the road was opened.

Inspection of Table I indicates four fairly distinct phases of weather during the season. I first arrived at Logan Pass on June 6, which was a cold and windy day with periods of sleet. Snow depths from five to twenty feet were estimated on the study area at that time. However, at the beginning of continuous observation on June 14, one week later, the weather was clear and had been for at least the preceding day. Clear and fairly warm weather predominated for the following week until June 20. This warm period resulted in a fairly constant melt of snowcover (about three inches per day) and an apparently related increase in territorial and courtship activity in the ptarmigan.

Cool, wet weather commenced on June 21 and lasted until July 8. This period was marked by fairly even, cool temperatures which usually remained above freezing. Considerable rainfall came during this period but, unfortunately, it could not be measured. Additional precipitation in some form occurred on thirteen of the seventeen days in this period. This large amount of moisture, plus the continuous above-freezing

weather resulted in a very rapid snow-melt. A drop in snow level of two and one-half feet in one week was recorded. Flooding of most of the snow-free ground as well as the normal watercourses was characteristic of this period. It was during this wet time that ptarmigan nested and began incubation throughout the Logan Pass area.

Five weeks of continuous warm, dry weather during July and early August constituted the real "summer" at Logan Pass. Precipitation was recorded on only one and one-half days from July 8 to August 11. Days were warm, nights were cool, and snowcover and average relative humidity became markedly lower each day. Even the ever-present winds diminished slightly. During this favorable period, plants flourished and ptarmigan broods hatched and underwent their first few weeks of growth.

The good weather was short-lived, however, and August 12 initiated a cold, wet period which continued for the remainder of the season. Precipitation during this final six weeks of the study measured 17.63 inches, or about three inches per week. Precipitation occurred on an average of over four days per week in the form of rain, fog, hail, and snow. By contrast, the wettest August and September recorded at the nearest weather bureau station, Belton (West Glacier), about twenty air miles southwest at an elevation of 3,100 feet, was in 1916 when 10.37 inches of rain fell in the sixty-one days. The first "autumn" snow fell on September first (one and one-half inches), but it soon melted. Some old snowpatches had not melted by this time. This extended snow-melt provided water which made young, growing plants available for ptarmigan food throughout the season.

However, a foot of snow which had fallen during the preceding nine

days lay on the level ground on October 4. The road was closed during the next week due to more snow, and presumably snow depth continued to increase after the last observation.

Plant Communities

Logan Pass cannot be characterized as a single ecological unit. Within its flora and fauna there are representative species which are usually considered characteristic of the tundra and taiga biomes, respectively.

Odum (1953) defines biomes as the largest land community unit convenient to recognize. These are areas where regional climate interacts with regional biota and substrate to produce large, easily recognizable units.

The northernmost biome, characterized by low temperatures and a short growing season, is the tundra. Isolated areas of tundra occur on cold mountain tops in more southerly regions.

The next warmest region is the northern coniferous forest or taiga biome which stretches across great areas in northern continents and southern extensions occur in most mountain ranges at elevations with similar physical conditions.

Pitelka (1941) shows an ecotone or transition area between tundra and coniferous forest on his biome map in the northern areas, but shows the mountains as having complicated zonation. Logan Pass lies in just such an ecotone.

Within this general ecotone at Logan Pass there is a number of smaller biotic communities which individually may be more or less like either biome, and some are probably unique to this area. These unique

communities are often characteristic of ecotones (the "edge effect," Odum, 1953).

Since these communities could not be analyzed in detail and their characteristic animals and smaller plants determined, they will be discussed as plant associations. A plant association is defined as a grouping of plants distinguished by certain dominant species, their characteristic life form and spacing. Successional and geographic relations are not considered in this small area.

Several plant communities have been suggested for the Logan Pass area by Sammons (MS). These communities have been modified by the author into plant associations which are shown on Figure 2. Associations cannot always be clearly differentiated, but usually can be recognized by their characteristic topography and moisture as well as by certain spermatophytic plants. Present knowledge does not allow determination of dominance among these characteristic plants.

Wet meadow. Moist, relatively level ground, particularly along the larger streams commonly develops a characteristic wet meadow association of plants. Sammons (MS) suggests the following species as characteristic: Elymus glaucus, Salix communtata, Anemone parviflora, Ranunculus eschscholtzii, var. exinmo, Mitella breweri, Saxifraga rhomboidea, Leptarrhena pyrolifolia, Parnassia fimbriata, Gentiana calycosa, Juncus mertensianus, Mimulus tilinqui, M. lewisii, Polygonium viviparum, Poa alpina, Senecio triangularis, Agrostis thurberiana, Carex tolmiei, C. kelloggii, Tofieldia gluminosa, and Kalmia polifolia.

— Ptarmigan are commonly found in the rockier portions of this community (where adequate cover is available) particularly during the

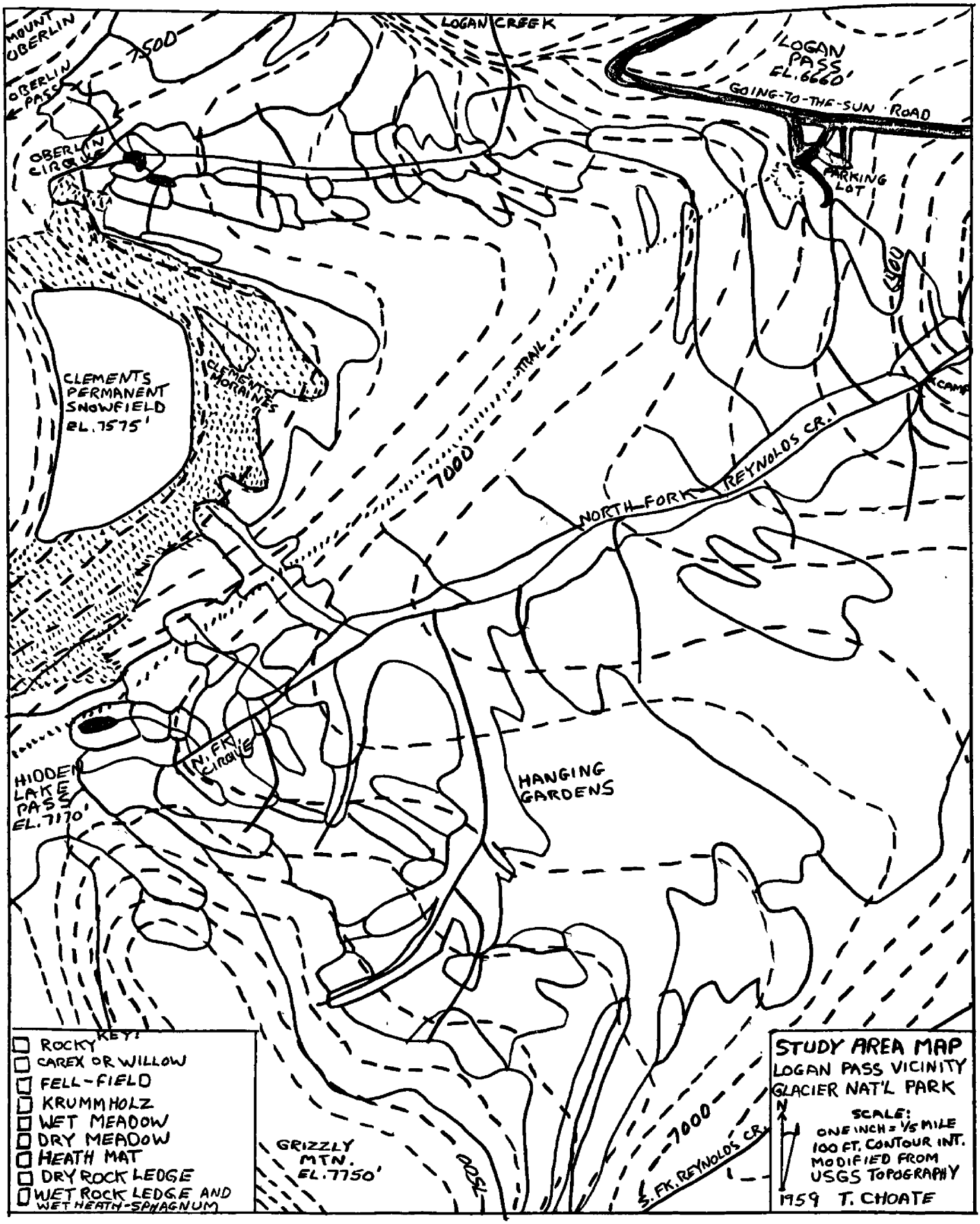

FIGURE 2. Preliminary map of plant associations

latter half of the season. This probably is because of the continually available, newly sprouting vegetation in this association.

Wet heath-sphagnum. Where moisture accumulates, particularly in bottom areas and behind rock ledges, boggy associations develop. In the two best developed bogs, hummocks up to a foot high of sphagnum, heath, or a comination of the two occur, resembling small "niggerheads" of northern muskeg areas. Sammons (MS) lists the following characteristic species: Cassiope mertensiana, Salix nivalis var. Nivalis, Poa arctica, Arnica cordifolia var. pumila, Taraxacum lyratum, and Sphagnum spp. Ptarmigan were rarely noted in this type, but this may be due to its rare occurrence.

Carex and willow associations. Certain small areas of moisture accumulation develop relatively pure stands of either Carex tolmiei or Salix commutata. The protected streambottom areas which develop these associations may occasionally be visited by ptarmigan early or late in the season. Carex is utilized by ptarmigan in the fall when the seeds have matured. Willow buds from these taller stands may provide an important source of food for ptarmigan during the winter and spring since they may project above the snow surface. Few individuals were noted in this association during the summer.

Dry meadow. Relatively level areas which are moderately well-drained support the dry meadow association. Extensive areas of benchland including low rock ledges and other areas of moderate soil development are covered by dry meadow. The soil is moist for about a month after the snow melts, but is dry by fall. Sammons (MS) lists the following typical

species: Luzula glabrata, Erythronium grandiflorum, Carex nigricans, Sibbaldia procumbens, and Hypericum formosum. Phleum alpinum and Erigeron peregrinus are usually present in smaller numbers. Ptarmigan were only occasionally seen in this association. A few males occupied rockier dry meadow territories temporarily in mid-July.

Wet rock ledge. A few rock ledges, because of moisture from snow banks or streams, are constantly wet, particularly on their shadier and steeper aspects. Although soil is very shallow in most cases, certain plants clump together to form associations which are frequently visited by ptarmigan. Characteristic species are Saxifraga mertensiana, S. debilis, S. adsendens, and Romanzoffia sitchensis (Sammons, MS). This association was most commonly used by males during the territorial period and by females with young broods for the first few weeks after hatching.

Dry rock ledge. Rock ledges varying in height from two to ten feet comprise a large portion of the study area including the sector known as the "Hanging Gardens." The tops of these ledges usually are from five to fifty feet wide and are covered by shallow, rocky soil which becomes dry by mid-August. The bases of these ledges may be moist and retain snow-banks until late July, especially on the north and east slopes. In 1959 these areas held snow two to three weeks longer than usual. Ptarmigan were noted on these ledges while they remained moist and young plants were available. Three species largely restricted to this association are Lewisia pygmaea, Vaccinium myrtillus, and Viola adunca. Other common species are Potentilla diversifolia, Sibbaldia procumbens, Ranunculus eschscholtzii, Senecio resedifolius and Antennaria alpina (Sammons, MS).

Krummholz. Small clusters of stunted to prostrate trees occur over about half of the study area, particularly on the eastern and southern borders. On the extreme borders and in a few sheltered spots along Grizzly Mountain, groups of scrub trees cover large areas and may reach a maximum height of twenty-five feet. Krummholz occurs on some ledges commonly used for courting and nesting territory by ptarmigan, but the birds rarely enter the trees except to escape a pressing enemy such as a human wielding a net. The species commonly comprising the krummholz association are Abies lasiocarpa, Picea engelmanni, Pinus flexilis, and occasionally Pseudotsuga taxifolia, Juniperus communis, Arctostaphylos uva-ursi, and Vaccinium membranaceum are commonly found under the better developed stands.

Heath mat. On relatively sheltered slopes or ledges of moderate moisture conditions, extensive mats of Phyllodoce may develop. Ptarmigan are frequently seen in this type in the spring when the snow has just melted and extensive new buds are available. One hen nested in a small clump of heath. In late fall and early winter, mats of heath are sometimes snow-free "islands" and may be used commonly by ptarmigan.

Fell-field. Very rocky ledges and slopes with very little soil development have a somewhat unique plant association. Many areas where snow persists and produces an extremely short growing season, and the edges of old moraine and scree, can also be considered fell-field. The characteristic plants of these variously formed fell-field areas include Dryas octopetala, Pentstemon ellipticus, Silene acaulis, Saxifraga bronchialis var. saximontana, Erigeron compositus, Phacelia sericea,

Arabia lyallii and Arenaria obtusiloba (Sammons, MS). Ptarmigan were observed in these areas when the vegetation first sprouted and occasionally thereafter.

Rocky. Areas where rock ground cover exceeds eighty per cent, including talus, scree, moraine, and some ledges and cliffs, develop a pioneer plant association. Conditions are usually dry and the area is often exposed to high winds. Ptarmigan seem to occur here only occasionally during the early and late weeks of the season when other areas are snow covered. Lichens are characteristic on the rocks and the small ground area commonly supports the following species: Myosotis alpestris, Potentilla fruticosa, Papaver nudicaule, Anemone globosa, Saxifraga bronchialis var. saximontana, Phacelia leucophylla, P. lyallii, Agropyron latiglume, Crepis nana, Agoseris aurintica, Arenaria nuttallii, Silene acaulis, Polemonium viscosum, Eriogonum flavum var. piperi, E. ovalifolium var. nivale, and Sedum stenopetalum (Sammons, MS).

THE PTARMIGAN POPULATION

Numbers

A total of 116 White-tailed Ptarmigan were banded during the 1959 season at Logan Pass. An additional ten birds were seen that could not be netted for banding. Unbanded ptarmigan were encountered continuously from the beginning to the end of the study. At the end of the first thirty days, 29 birds had been banded. By the forty-fifth day 59 had been banded and this total reached 111 at the end of sixty days of observation (see Figure 3). Twenty-nine more were banded at locations in Glacier Park outside the study area, making a total of 145 banded individuals.

Individual ptarmigan were re-observed on as many as thirty-eight days and some were never seen after their initial banding. Some color band combinations were not always visible, making some observation records questionable, and a few observations by other observers were made. Therefore, both maximum possible (including these questionable observations) and minimum figures (clearly identified by me) for ptarmigan observations appear in the following table.

TABLE III. Observations on individual White-tailed Ptarmigan

	Maximum Possible	Minimum
Total observation-days, all ages	765	618
Average number of re-observations per bird	6.6	5.2
Average number of observed birds per day	7.5	6.1

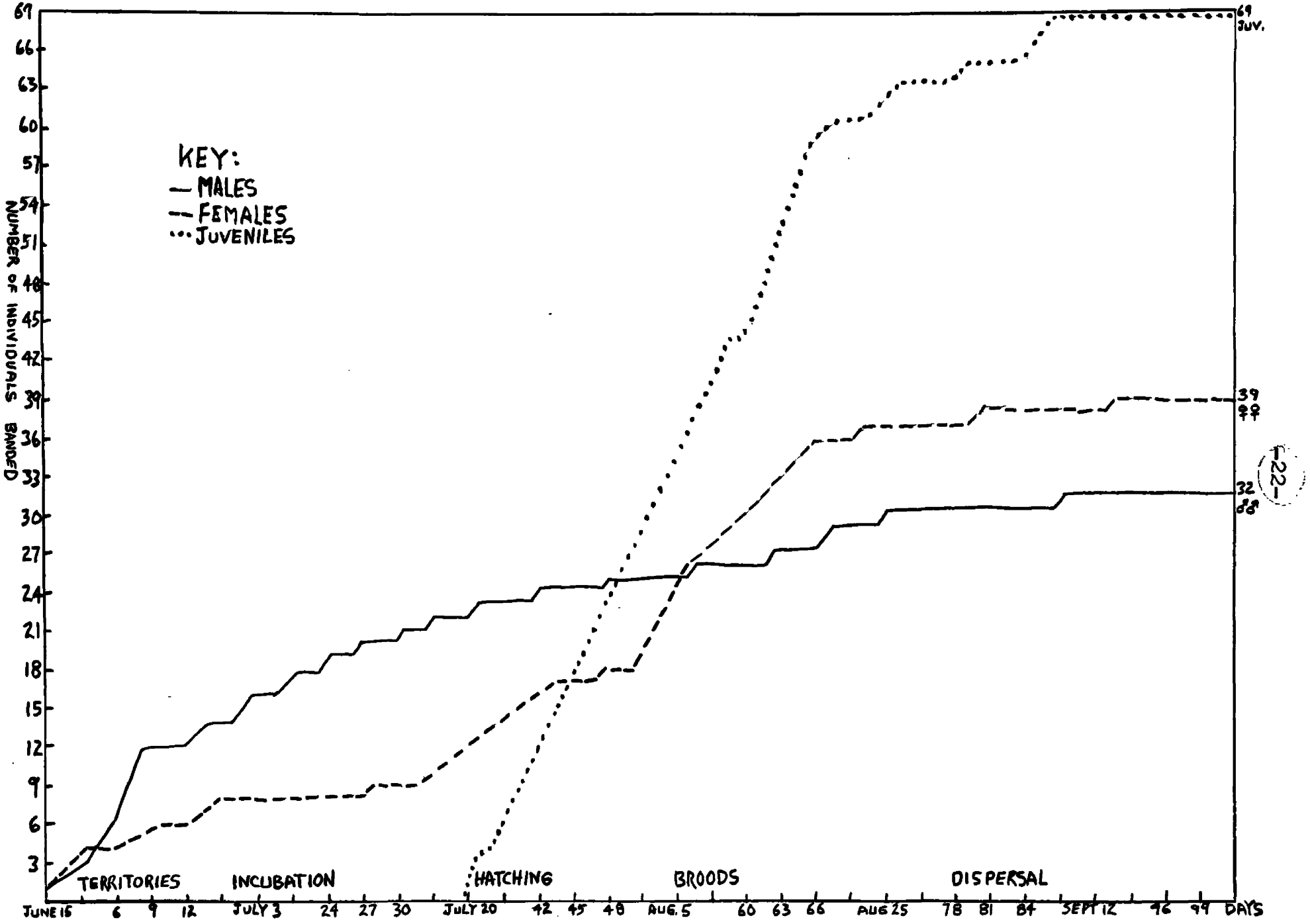

FIGURE 3. Cumulative observations (bandings) of ptarmigan at Logan Pass in 1959.

Each banded ptarmigan was re-observed an average of six times over the study period of 102 days. This figure is deceivingly low, due to the inclusion of young which were first observed in mid-season and had a higher mortality rate than the adults. An average of seven ptarmigan were seen per day of observation.

Composition

Of the 116 ptarmigan banded at Logan Pass, sixty-eight were adults (thirty-two males, thirty-six females). The remaining forty-eight birds were unsexed chicks.

The composition of the sixty adult ptarmigan seen during the first seventy-five days of observation was twenty-nine cocks and thirty-one hens. These sixty adults plus forty-seven chicks observed during the fifty-six days after hatching date (July 26) comprise the total ptarmigan which were re-observed during the study. Males, females, and chicks were not re-observed in equal proportions, and some individuals were never re-observed after banding. Table IV is an analysis of observations on each class of birds comprising the population. An observation is considered an observation-day and vice versa whether the individual was seen once or several times on that day. Number of birds per day refers to the days of the above re-observation periods (seventy-five and fifty-six days).

TABLE IV. Observations on ptarmigan by composition classes

	Males	Females	Chicks
Total number of observation-days	274	280	189
Average number of re-observations per bird	9.45	9.03	4.02
Average number of observed birds per day	3.6	3.7	3.4

The lower number of re-observations on chicks is due to the shorter observation period and perhaps a higher mortality rate.

Changes in Numbers and Composition

Total cumulative observations of different individual ptarmigan are shown on Figure 3. One hundred thirty-six birds were seen by the one-hundredth day of observation (September 22); of these sixty-seven were adults and sixty-nine were chicks.

The changes in relative numbers of total females, males, and chicks observed were quite marked. During the initial fourteen days (from June 15 to June 29) many males and a few females accompanying them were seen on territories. During the following twenty-one days (from June 30 to July 20) which was the incubation period for most females, few were seen. New males were encountered regularly during this period, many occupying new territories without females. Hatching of chicks commenced about July 20 and was complete two weeks later. During this period many hens were observed, usually accompanied by four chicks. During the next two weeks, until August 17, observations were primarily of broods of several

chicks which kept close to the mother. After this time the chicks could fly well and would often venture long distances from the mother.

During this dispersal period, increasingly fewer chicks were seen in broods and few new broods were observed. A slight increase in males seen at mid-August was probably due to cessation of territoriality and the beginning of fall flocking by adults in areas of abundant food. Flocking increased to a peak in mid-September. Although an average of 7.5 birds were seen per day throughout the study, extremes of forty-six (September 8), forty-three (September 15), and fifty-seven (September 19) were observed.

Chick mortality (not indicated by the graph) totaled only twenty-three per cent in nine broods (thirty-two chicks) observed over an average period of 47.3 days during the late summer-fall period (August and the first half of September). (See also Table X.)

When the re-observations of adult ptarmigan are analyzed by the Schnabel Method (1938), a slowly increasing population figure is obtained. At the end of July this method indicates a population of twenty-seven ptarmigan. The large numbers of ptarmigan observed during September raised the calculated population to forty-nine for the season. This figure is probably an accurate index of the "resident" population of the study area. Even though the population clearly fluctuated during the study period, a general increase in total numbers was evident (see Table V).

TABLE V. Adult ptarmigan population by the Schnabel Method

1959 Date	Total Ptarmigan Seen (S)	No. (M) Prev. Banded	No. (R) Banded Seen	MS	MS	R	P= $\frac{MS}{R}$
June 16	4	3	1	12	12	1	12
19	5	6	3	30	42	4	10.05
20	4	8	2	32	74	6	12.33
21	2	10	1	20	94	7	13.42
23	7	11	2	77	171	9	19.00
25	5	16	4	80	251	13	19.30
26	3	16	3	48	299	16	18.68
28	6	16	3	96	395	19	20.78
29	4	20	3	80	475	22	21.70
30	8	20	8	160	635	30	21.16
July 1	5	20	5	100	735	35	21.00
2	7	20	7	140	875	42	20.83
3	7	20	5	140	1,015	47	21.59
4	5	22	5	110	1,125	52	21.63
6	9	22	9	198	1,323	61	21.68
8	12	24	12	288	1,611	73	22.06
10	3	25	3	75	1,686	76	22.18
13	9	25	7	225	1,911	83	23.02
15	9	27	8	243	2,154	91	23.67
17	5	31	5	155	2,309	96	24.05
20	9	31	8	279	2,588	104	24.88
22	4	33	3	132	2,720	107	25.42

TABLE V (continued)

1959 Date	Total Ptarmigan Seen (S)	No. (M) Prev. Banded	No. (R) Banded Seen	MS	MS	R	P= MS/R
July 24	2	34	2	68	2,788	109	25.58
26	4	34	3	136	2,924	112	26.10
29	1	36	1	36	2,960	113	26.19
31	4	36	2	144	3,104	115	26.99
Aug. 3	1	41	1	41	3,145	116	27.11
6	6	41	6	246	3,391	122	27.79
8	7	46	7	322	3,713	129	28.78
11	16	49	15	784	4,497	144	31.22
13	3	51	1	153	4,650	145	32.06
17	6	54	5	324	4,974	150	33.16
21	4	58	4	232	5,206	159	32.74
23	8	58	7	464	5,670	166	34.16
26	5	60	5	300	5,970	171	34.91
29	3	60	3	180	6,150	174	35.34
Sept. 1	2	60	2	120	6,270	176	35.62
3	6	60	6	360	6,630	182	36.42
6	6	60	6	360	6,990	188	37.18
8	10	60	10	600	7,590	198	38.33
11	32	60	32	1,920	9,510	230	41.34
14	21	62	21	1,302	10,812	251	43.07
16	18	62	17	1,054	11,866	268	44.27
19	37	63	36	2,331	14,197	304	46.70

TABLE V (continued)

1959 Date	Total Ptarmigan Seen (S)	No. (M) Prev. Banded	No. (R) Banded Seen	MS	MS	R	$P = \frac{MS}{R}$
Sept. 22	19	64	19	1,216	15,413	323	47.71
23	12	64	12	768	16,181	335	48.30
Oct. 3	4	64	2	256	16,437	337	48.77
4	5	66	4	330	16,767	341	49.17

TERRITORY

A territory is here defined as that area of ground occupied or defended by a male ptarmigan for a period of at least two days. Practically no information has been published on the territorial behavior of White-tailed Ptarmigan. Lewis (1904) very briefly mentions fighting between males. No author specifically mentions an area occupied as a territory by males, although it is implied by certain descriptions in Bradbury (1915), Lewis (1904), and others.

Courtship calls (possibly territorial) are mentioned in Bailey (1905) and Packard (1945), and are probably the calls described in Bradbury (1915). Pairing and defense of the mate are mentioned by three authors in brief statements (Packard, 1945; Dawson, 1909; Bradbury, 1915) and brief discussion of courtship occurs in Weeden (MS).

No territorial information was gathered in the previous study at Logan Pass in 1958. In 1959 observations on the individually color-marked birds provided evidence of territoriality. Probably male White-tailed Ptarmigan occupied some area as a territory at least briefly during the main period of territorial activity, from mid-June to mid-July, 1959. However, only a few males (seven or eight) were observed to consistently exhibit territorial behavior during the mating period in mid- or late June. Many more broods were observed than could be accounted for by territories, even if each was visited by more than one female. Paired birds were observed which never were identified with territories. Therefore, not all males are territorial and not all mating occurs in conjunction with territories, but probably

territoriality plays an important role in ptarmigan reproductive behavior.

Physical Characteristics

A total of thirty-three areas were observed to be occupied by male ptarmigan as territories at Logan Pass (see Table VI). The size of the area occupied varied from 10 x 15 to 80 x 30 yards, averaging 44 x 25 or 1,100 square yards. Boundaries are only approximate and were usually delineated by the surrounding snow or the observed movements of the male (see Figure 4).

No significant change in size was noted between territories established progressively later in the season, nor was there an observed relationship between size and location, physical, or biological characteristics of the territory. Variations in size may be related to the aggressiveness of the occupying male and the amount of suitable area available.

Every territory is characterized by the presence of broken rock masses, usually in the form of the rock ledges and remnant boulders formed by resistant strata on the predominant Cambrian argyllites. The presence of rock on every territory may be related to a protection requirement of these birds. Ptarmigan were rarely seen in areas without rocks which could be used for camouflage.

TABLE VI. Characteristics of ptarmigan territories observed at Logan Pass in 1959

Terr. No.	Location General Area	Estimated Size in Yards	Topography	Water	Plant Associations	Changes
1	Oberlin Basin	90 x 20	high ledge and cliff	several rivulets and snow	wet ledge, krummholz, heath	temporary eastward expansion to areas 1a & b 6/28-7/3
1a & b	south side Oberlin Basin	30 x 20 10 x 20	rock ledges	snow	similar and dry ledge	occupied 6/14-7/26
2	head of North Fork	40 x 15	wide ledge and narrow ledge	one rivulet, snow, spring	wet ledge, fellfield, heath	none, intermittent use
3	Oberlin Basin	70 x 20	wide ledge and sloping ledge	one stream, snow	wet ledge, dry ledge, krummholz	none, occupied 6/16-25 (see #9)
4	foot of North Fork	20 x 30	cliff, small ledge, open	large stream, snow	krummholz, dry ledge, wet ledge	none, intermittent use
5	Oberlin Basin	25 x 20	low ledge, open, rocky	rivulet, snow	krummholz, dry meadow, dry ledge	radial expansion as snow melted to 5a & 5b. Use not continuous 6/20-7/31
5a & b	lower slope Oberlin Basin	expanded to 75 x 40	similar	similar	wet ledge in 5a and 5b	
6	head of North Fork	40 x 50	large low ledge	snow	fell-field, heath, krummholz	none, temporary use

TABLE VI (continued)

Terr. No.	Location General Area	Estimated Size in Yards	Topography	Water	Plant Associations	Changes
7	Grizzly Mountain	20 x 25	steep ledge and sloping ledge	rivulet, snow	fell-field, heath dry ledge	occupied 6/23-30 temporary movement Se to 7a 7/1-3
7a	Central Mountain	35 x 30	sloping ledge and open slope	similar	krummholz, heath mat	
8	Grizzly Mountain	80 x 25	two ledges, 8a	two rivulets, snow	dry rock ledge, wet ledge	occupied 6/23-7-5
8a	South	60 x 40	sloping small ledges	one stream, snow	heath, krumm-holz	movement NE to 8a 7/6-18
9	Oberlin Basin	40 x 30	moraine slopes ledge	small stream pond and snow	fell-field, dry ledge, krummholz	none, may be expansion of 3 occupied 6/26-7/10
10	Oberlin Basin	35 x 15	two high ledges	snow	fell-field, dry ledge	none, temporary use
11	Oberlin Basin	25 x 10	small sloping ledge	snow	dry ledge, krumm-holz	none, temporary use
12	head of North Fork	40 x 40	five high ledges	stream, snow	dry ledge, wet ledge, krummholz heath	occupied 6/29-7/6

TABLE VI (continued)

Terr. No.	Location General Area	Estimated Size in Yards	Topography	Water	Plant Associations	Changes
12a	head of North Fork	15 x 10	high ledge	snow	dry ledge, fell-field	movement SE via 12a to 12b
12b		15 x 20	low ledge	rivulet, snow	wet ledge, willow	7/7-12
13	Hanging Gardens	30 x 25	broad low ledge	two rivulets, snow	dry rock ledge, heath	none, temporary use
14	Grizzly Mountain	25 x 20	narrow ledges and talus	snow	dry ledge, rocky	intermittent use 14a later
15	Oberlin Basin	75 x 25	wide sloping ledge and rock	two rivulets, stream, ponds, snow	dry ledge, wet ledge, krummholz	7/4-23 use non-continuous some movement to E. to 15a 7/24
16	foot of North Fork	30 x 30	rolling ridges, small ledges	large stream, snow	wet meadow, dry meadow	none, intermittent use
17	head of North Fork	40 x 25	three high ledges	several rivulets snow	wet ledge, dry ledge, krummholz	use non-continuous 7/6-7/29 none
18	Hanging Gardens	80 x 30	large, flat ledge	one rivulet, snow	dry ledge. dry meadow, krummholz	7/7-12 use not continuous. To 18a movement S, temp. 7/13

TABLE VI (continued)

Terr. No.	Location General Area	Estimated Size in Yards	Topography	Water	Plant Associations	Changes
19	Grizzly Mountain	10 x 15	small ledge	snow	dry ledge, krumm-holz	none, temporary use 7/7
20	head of North Fork	40 x 20	two high ledges and cliff	rivulets, water-fall, snow	wet ledge, krummholz, mosses	none, 7/7-13 non-continuous use
21	Oberlin Basin	50 x 30	long ridge and low ledge	snow	dry ledge, krummholz	none, temporary use 7/7
22	foot of North Fork	35 x 15	long ledge, rocks	snow	dry meadow heath	none, intermittent use
23	foot of North Fork	30 x 30	two ledges, ridge and rocks	large stream snow	wet meadow dry meadow	intermittent use 23 and 23a same
24	Oberlin Basin	70 x 25	two sloping ledges	snow, one rivulet	dry rock ledge	none, temporary use 7/8
25	Hanging Gardens	50 x 40	wide flat ledges	snow	dry rock ledge	25 and 25a temporary use
26	head of North Fork	20 x 15	ledges	snow	wet ledge, dry ledge, heath	none, temporary use 7/10 and 15

TABLE VI (continued)

Terr. No.	Location General Area	Estimated Size in Yards	Topography	Water	Plant Associations	Changes
27	Hanging Gardens	50 x 30	two rock ledges	stream, water-fall, snow	wet ledge, dry ledge, wet meadow	temporary use 7/12. 27a
27a		50 x 20	rock ledge	similar	similar	intermittent use 7/15-21
28	Hanging Gardens	60 x 35	two wide ledges level	rivulet, snow	wet ledge, dry ledge, wet meadow	none, temporary use 7/13
29	Grizzly Mountain	26 x 15	two steep ledges	snow	dry ledge, heath, krummholz	none, temporary use 7/13
30	below Oberlin Basin	50 x 30	ridge, two ledges	snow	dry rock ledge, krummholz	none, temporary use 7/20
31	below Oberlin Basin	40 x 35	three sloping ledges	snow	dry rock ledge	none, temporary use 7/20
32	below Oberlin Basin	55 x 30	several broken ledges	snow, rivulet	dry rock ledge	none, temporary use 7/20
33	edge of Oberlin Basin	85 x 15	high rock ledge and cliff	rivulet, snow	wet ledge, dry ledge, krumm-holz	none, temporary use 7/21

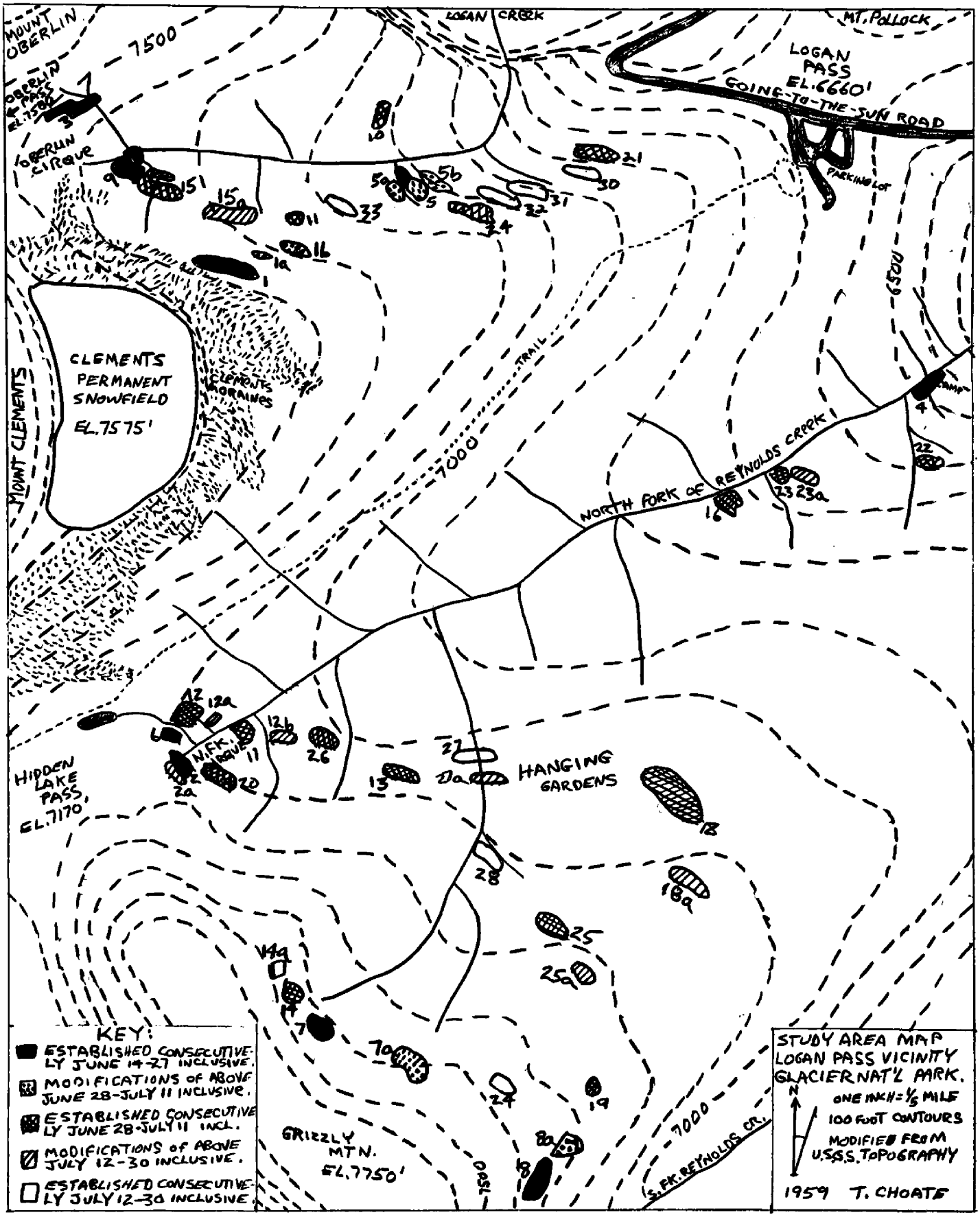

FIGURE 4. Location, sequence of establishment, and changes in territories occupied by male White-tailed Ptarmigan

Water appears to be another necessary factor in ptarmigan habitat and characterized all territories occupied. Those areas having streams, rivulets, or other semi-permanent water sources were those most consistently occupied. All areas initially were "islands" of rock surrounded by snow which supplied water at least temporarily. But those areas which were moist longest, and therefore contained at least some moist, fresh vegetation over a long period, were the territories used longest and which were most often visited by females.

Biological Characteristics

All territories contained ledges and therefore had at least some development of the ledge plant associations (see Table VI). Every area not just temporarily occupied had fairly extensive development of the dry ledge association. The continually occupied areas (1, 3, 7, 9, 12; see Table VI and also page 39) all had combinations of wet ledge, dry ledge, heath patches, and krummholz (for detail, refer to pages 15 to 20). This combination probably best provides the plant species preferred for food and cover.

Krummholz and heath both were observed to provide shelter from winds for territorial males. Heath buds were a commonly utilized food during the early or establishment phase of territoriality.

The wet ledge association seems to prove a long-lasting source of certain preferred mosses and succulents as well as the more temporary green shoots and buds. The dry ledge association appears to contain a number of plants whose green shoots are preferred by ptarmigan. The dry ledge association is utilized a great deal in its early, moist stages and thus may be an important part of the territory which is

typically occupied as soon as the snow melts.

Establishment

Territories were established continually throughout the territorial period from June 14 to July 20. However, the last continually-occupied territory was established June 29. Territories established in July were generally used only occasionally or for short periods, and females were usually not associated with them. Most territories were established as soon as suitable areas became exposed above the snow, and occasionally expanded or changed as snow melted and better areas became available.

The establishment procedure was not clearly determined, but it may take several forms. On two occasions paired birds were seen flying to open ledges as if "inspecting" their merits as territories. In both cases the male gave a screaming call upon landing. This call is similar to the one given by a male in courtship flight, when very excited, or in answer to another male. In one of these two cases a male on a territory 150 yards away answered the call and became very excited. Calls were exchanged between the males twice more following this, but no fighting was observed.

In a third case a pair of ptarmigan was observed walking toward the center of a territory already occupied by another pair of birds. A few minutes later screams were heard and the resident male pursued the intruding male in flight some distance from the territory before returning. The new female was either ignored or not seen by the resident male.

From these three observations and the regular occurrence of new

males on newly opened territories or potential territories, I postulate the establishment of territories to be as follows:

The male looking for a suitable territory, whether in the company of a female or not, visits available areas both on the wing and on foot. If he does not encounter a resident rival male on the area either by contact or response to the "scream," he occupies the area temporarily or permanently, depending on its suitability. Since males on non-permanent territories were observed to answer calls of other males, it is assumed that they take possession of the area immediately upon finding it unoccupied.

Only twice were two males observed on the same ledge without one appearing to be a dominant resident and driving other males away. In both cases the males appeared to be "testing" or establishing a boundary between two adjacent territories.

From the above observations and lack of observed fighting, I interpret the establishment of territories to be primarily a "first-come-first-served" operation, rather than the result of dominance or the outcome of a fight between two males.

Maintenance

Time and area. The thirty-three territories are divided into three categories: those maintained continuously (#1, 3, 7, 8, 9, 12); those maintained intermittently (#2, 4, 5, 14, 15, 16, 17, 18, 20, 22, 27); and those established briefly or maintained only temporarily (#6, 10, 11, 13, 19, 21, 24, 25, 26, 28, 29, 30, 31, 32, 33).

Of the six continuously occupied territories, the longest occupation period was forty-two days (#1), the shortest ten days, and the

average almost twenty days (see Table IV). Four of these six males changed the location of their territories toward the middle of the territorial period. Three of these four changed territories were occupied only temporarily and finally abandoned. The fourth (#1a and 1b) was occupied temporarily followed by reoccupation of the old territory with a new female. In each of these four cases the change can be related to the influence of the female of the pair. In two cases the female left the territory of the male for nesting elsewhere (1b and 12b); in one case the female was killed (7); and in the last the female abandoned one male's territory (8) for another and the male subsequently occupied a nearby new area (8a) with a new female. It would appear from these observations that the male occupies a fairly fixed territory, but that the territory may change if the male takes on a new mate. The female's adherence to the territory is weaker than that of the male.

Areas considered to be intermittently occupied had observed use at least two times for a total of at least four days. Of the eleven intermittently occupied areas, the longest continuous occupation period was four days. However, one territory (#5) was occupied by two different males for a total of fourteen days over the whole territorial period of approximately forty days.

A few of these territories changed in size and location, the most notable of these being #5 which tripled in size as area became available and also showed some temporary changes in location. Most areas, however, were not occupied long enough to show a distinct pattern of change.

The remaining fifteen territories were occupied for periods of four days or less and not revisited for more than one day. These are

territories of minor importance and show no pattern of change in area or location.

Defense. Actions considered to be defense of the territory were observed on eleven occasions. Actual fighting between males was only observed on three occasions. All three of these cases were in the early period of territoriality when mating was taking place (June 19, 23, 25) which is probably the period of most intense fighting. Weeden (MS) suggests that testis development is at its maximum during this period.

Two of the three cases of fighting consisted of the resident male driving off an intruding male. However, the status of the two males had not been previously determined in one case. The first sign of defensive action was the "scream" call which was usually followed by a short series of loud clucks vaguely resembling an amplified, reversed call of the domestic hen.

The call of one cock seemed to excite and elicit immediate retort by the other, regardless of their position as dominant, intruder, or resident. However, in all three cases of observed fighting, one male appeared from the beginning to be dominant and in two of the three cases this was known to be the resident bird. The scream-call of the rival male was observed to elicit an attack behavior from the resident male who flew or ran rapidly straight at the rival. In two cases this resulted in the intruder taking wing off the territory, with the resident male in close pursuit.

The pursuit flight began with a scream from the resident male and occasionally one from the intruder. Flight was strong but erratic, with the pursued bird often dodging attacks in flight. Distance covered by the

pursuit flight varied and often followed a somewhat curved path, but in these observations it averaged slightly over one hundred yards. Once both males were observed to land, followed by a single, short, running attack by the resident male. However, more resistance by the intruder may have been met, for the resident then took off with a scream and flew directly back to his mate on the territory.

The third observed case of fighting began similarly but the intruding male would not leave the territory and tried to avoid the rushes of the dominant bird. At first it appeared that the intruder was trying to reach a female ptarmigan some twenty yards away on the territory. Her status as a resident was undetermined; she stayed on that territory at least one day, but was seen on another male's territory a few days later.

After three or four rushes by the dominant male the intruder made a few brief attacks of his own, creating the only real battle observed during the encounter. The battle lasted approximately thirty seconds and was characterized by much squawking, wing-flapping, and jumping about. At the end of this brief skirmish the intruding bird suddenly took flight with the resident in close pursuit, leaving a few feathers behind as the only evidence of injury.

The intruding bird proved to be very persistent and led his pursuer in a wide circle, terminating on the territory near the female. However, the dominant bird landed with a scream directly behind the intruding bird and attacked immediately. This time there was less resistance and a second pursuit flight took place within a minute.

The intruding bird returned again to the territory but was soon driven off as before. This process was repeated five times while the observer was present, the birds taking momentary rests between encounters

in the last "round." After the fifth pursuit flight the dominant male returned to the territory alone, landing near the female with a scream-call which aroused her from a resting pose and her seeming indifference to the previous thirty-minute fight.

During this fighting the two males appeared completely oblivious of everything except the other male. Rain and sleet fell continuously and in the middle of the third "round" on the territory I approached the males with a hand-net to capture them for banding. Neither bird seemed to notice me until I was within eight or ten feet and then merely pursued each other in a general direction away from me. When my attempt on a running bird (the intruder) at a distance of six feet failed to net him, the dominant male made an attacking run around me to get at the other male. Both birds were subsequently captured and banded, the intruding male being released first. This male ran about twenty feet from me, ruffled his feathers, and began to rearrange them, showing much less fear than the average released bird. When the dominant male was released he, too, ran only a few feet, then he spotted the other male and immediately attacked, resulting in the fourth "round" and pursuit.

The significance of this single series of events cannot be clearly determined, but the fact that there was a female present and that this same "intruding" male was found occupying an extension of this same territory about eighty yards from the "dominant" male two days later may make this a somewhat complicated case.

All of the remaining eight defense observations concerned sound stimulation rather than the visual stimulation of fighting recorded above. In all cases the call of another male excited the resident male to the extent of screaming back and giving "annoyance clucks." Some males

flicked the tail and craned the neck in the direction of the sound. These actions are typical of disturbed birds and were regularly shown toward the observer upon close approach or when being released after banding.

One male, excited by a rival's call, flew in the direction of the rival to a high rock just beyond the boundary of his usual territory and gave two loud screams from there. Still another male was off his old territory near his nesting mate when he heard a scream from a rival male. He became excited and took off with a scream, flying directly to a prominent point on his old territory from which he screamed again.

—Observed territorial defense was evoked by either sound or sight of the rival male, with sight provoking actual fighting and pursuit.

The dominant males possessed no observable difference in physical stature from other males, but two of them were observed to have a whiter → or earlier plumage phase than the "intruding" rival. The males have a distinct black-and-white breeding plumage at the peak of territoriality which appears to be an arrested molt from winter to summer plumage. As the later phase of territoriality begins (about the time the hens are laying, the first of July in 1959), the males begin to lose more and more of the white winter feathers and by the end of the period are beginning to show autumn feathers. The whiter birds are therefore probably closer to the middle of their individual territorial periods and the peak of testis development. This suggested relationship is based on Weeden's (MS) finding that testis size of male White-tailed Ptarmigan reaches maximum at the time the hen is laying eggs, about June first in his study, and declines thereafter. A relationship between the whiter birds and the more dominant, territorial individuals may therefore be present

but is not adequately supported by the small sample of observations in this study.

No defense activity was observed which was directed at anything other than male ptarmigan. Strange female ptarmigan were ignored or sometimes even courted. One case of a male with two females on his territory was observed. No defense by the female on a male's territory was observed directed toward either male or female ptarmigan, or toward other animals. Contacts were observed between territorial male ptarmigan and hoary marmots, ground squirrels, chipmunks, and man. Nutcrackers robbins, rosy finches, and hermit thrushes were observed on ptarmigan territories. Pipits and white-crowned sparrows even nested on occupied territories. Male ptarmigan paid no attention to any of these animals and even ignored a wolverine and a grizzly bear which in each case was within thirty feet. However, territorial males were observed to duck for cover at the approach of a golden eagle or a threatening observer.

Changes in defense and reoccupation. Two males occupied territories sufficiently long (over twenty-eight days) for changes in degree of defense to be observed. One male which drove away another in a pursuit flight of over one hundred yards on June 19 became very defensive at the sound of a call on June 25. However, he tolerated another male on the edge of his territory with his old mate on July 4 and had lost his female to another male's territory by July 7. This same male had a few autumn feathers by July 14 and was replaced by another pair on his territory July 16.

The other male had a considerably later territorial cycle, but this may have been because he obtained a second mate. This male defended his

territory consistently from June 14 to June 28 when he left the territory in company of his mate which was establishing a nest on another ledge. He defended her (at her call) from another female (see Page 58) and showed defensive responses to male calls, once flying back to the old territory to defend it. After his old mate began incubating he was again seen on his territory with the above "intruding" female as a second mate from July 4 to 16. During this period he was observed to respond to a rival call once. From July 17 to 24 he was not seen on his territory and was observed once one hundred yards away from it. On July 25 his second mate was observed on another male's territory, but on July 26 he was observed a final time with still another female. However, when this last observation was made the male was off his old territory.

— Insufficient information is available to determine changes in defense by males, but a decline in defensiveness, possibly correlated with testis size and related plumage, is suggested.

Two males occupied old territories with new females after their first mates had left the area. Two others occupied new territories with new females. This re-mating may reactivate territorial behavior and possibly arrest testis decline at least temporarily.

- No occupation of territory was observed other than during the mating period. However, in early September when large flocks were seen together and on the last day of observation, October 4, an increase in screaming by male ptarmigan was noted and some excitement of one male by the call of another was observed. The significance of these changes could not be determined.

Territorial Use

Table VII shows the observed use of the thirty-three areas designated as territories. Only twenty-two different males occupied the thirty-three areas because of movements between territories. More suitably located areas, or those where female ptarmigan were present, are suggested causes of these movements.

An average of 5.27 observed days of territorial use per male was recorded. Each territory was occupied an average of 3.51 observation-days by males and 1.93 days by females for a total observed ptarmigan-day-use of 5.45 per territory. Fourteen different females were observed on these territories and each spent an average of 4.57 observed days on them. The total period during which ptarmigan were observed on the territories varied from forty-two days on the most-used territory to a single day of observed occupation on some temporary areas. The average observed period of use for the thirty-three areas was 9.18 days.

Data on the average amount of the day spent by a male on his territory is very incomplete because few complete days of observation were made on a single individual. In three separate cases males were observed continuously for over eight hours on their territories. All three males moved only a short distance - about one hundred feet - during this period, each had a mate with him, and neither the male nor the female moved much, both being constantly within approximately ten feet of each other. Periodic feeding and resting of both birds at fifteen to thirty minute intervals was characteristic of each of the three observations, and many other shorter observations. Many males were re-observed as many as five times during a day and if the above pattern of little

TABLE VII. Observed use of territories by ptarmigan at Logan Pass in 1959

Terr. No.	Using	Dates Observed	Total Days	Using	Dates Observed	Total Days	Grand Total Use in Days*	Remarks
1, 1a, 1b	511	6/14,16,19,23, 26,28,29,30 7/1,2,4,6,8,9, 14,15,16,26	18	505	6/16,22,23,28, 29,30 7/1	8	36	505 nested at 1b starting 6/28
				519	6/30 7/1,2.4, 6,8,9,14,15,16	10	(42)	area 1 reoccupied with 519 7/2
2, 2a	501	6/15 7/6,7,16	4	502,532	6/15 #32 7/16	2 (1 ea.)	8(30)	7/16 observation of pair on 2a
	?	7/3	1	506	7/3	1		unknown male with 506
3	503,07	6/16,19,20,26 6/19	4 + 1	504,06	6/16,19,20,26 6/19	4 + 1	10(11)	pair 6 & 7 "intruded" 6/19
4	509	6/20,28	2				2(9)	
5, 5a,b	508,18	6/20,28 7/2,7, 15,17,22,25	1 + 7	519	7/25	1	10	variable boundaries of these areas
	555	7/31	1				(41)	
6	510	6/21	1	506	6/21	1	2(1)	
7, 7a	513	6/23,25,30 7/2	4	517,14	6/23,25 6/25	3	7(9)	517 killed in laying condition

TABLE VII (continued)

Terr. No.	Using	Dates Observed	Total Days	Using	Dates Observed	Total Days	Grand Total Use in Days*	Remarks
8, 8a	516	6/23,25 7/2,6,7, 8,13,16,17	9	514	6/23	1	18	515 & 516 fighting on 6/23
	515	6/23,25	2	504	7/6,7,8,13,16,17	6	(24)	8a used by 516 & 504 7/6-17
9	503	6/26,30 7/1,2,3, 4,7,8,9	9	504	6/26,30 7/4	3	12(14)	this area may be an extension of #3
10	518,20	6/28/6/28	2	519	6/28	1	3(1)	
11	520	6/28	1	519	6/28	1	2(1)	
12a,b	510	6/29,30 7/1,3,6, 7,8,10	8	521	6/29,30 7/1, 3,6,7,8,9,10	9	17(12)	moved to 12b to nest 7/7
13	522	7/3	1				1(1)	
14, 14a	523,26	7/3/7/9	2				2(1)	
15a	511	7/4,6,14,15,24	5	504,519	7/4 7/6,14,15	1 + 3	12	
	531,503	7/16/7/19	1 + 1	530	7/16	1	(20)	
16	509	7/6	1				1(1)	

TABLE VII (continued)

Terr. No.	Using	Dates Observed	Total Days	Using	Dates Observed	Total Days	Grand Total Use in Days*	Remarks
17	501	7/6,29	2				2(23)	
18,18a	524	7/7,8,13	3				3(6)	
19	525	7/7	1				1(1)	
20	501,523	7/7,9/7/13	2 + 1				3(6)	
21	?	7/7	1				1(1)	not caught
22	509	7/8,9	2	506	7/15	1	3(7)	
23a	507	7/8,9,13	3	527	7/13	1	4(5)	
24	518	7/8	1				1(1)	
25	525	7/9	1				1(1)	
26	510,501	7/10 7/15	1 + 1				2(5)	
27,27a	522,524 525	both 7/12 7/15, 20	2 + 2	529	7/15,20	2	6(8)	522 and 524 conflicted and left 7/12
28	522	7/13	1				1(1)	
29	528	7/13	1				1(1)	
30	508	7/20	1	506	7/20	1	2(1)	

TABLE VII (continued)

Terr. No.	Using	Dates Observed	Total Days	Using	Dates Observed	Total Days	Grand Total Use in Days*	Remarks
31	518	7/20	1				1(1)	
32	518,520	7/20 7/31	1 + 1	538	7/20	1	3(11)	may be continuous with 31
33	540	7/21	1	539	7/21	1	2(1)	
TOTAL	22	6/14-7/31	116	14	6/15-7/25	64	180	days period
AVERAGE		per male	5.27		per female	4.57	5.45	9.18
		per territory	3.51		per territory	1.93		

*Figures in parentheses represent period of days during which use occurred

movement is typical, then male ptarmigan on well-established territories spend almost all of their time on these areas, doing relatively little moving during a day or even a period of several days.

—In early and late parts of the territorial period males were observed to spend more time off the territories. In the early period food requirements may not be met on the territory due to abundance of snow. In mid-June pairs of ptarmigan were twice followed by their tracks in the snow as they made circuitous trips extending about one hundred yards from the territories. These trips indicated extensive feeding by the pair on insects blown onto the snow. By mid-July, the majority of territorial males were shifting areas and spending much less continuous time on their territories than they did two weeks earlier.

Evening flights, usually of a courtship nature, may take both the male and female ptarmigan off territories for a few minutes, as may the similar dawn flights. However, it was not definitely established that the males which take these flights are necessarily those occupying a territory. Only once was a male ptarmigan occupying a permanent territory observed to fly at dusk. This male was not observed later that evening, but occupied the territory the following morning, and had probably roosted on the area. One other male, occupying a temporary territory, disappeared from that location at dusk and had not returned one hour later after dusk, and probably left permanently.

—From these few observations I suggest that male ptarmigan, occupying territories other than just temporarily, spend practically all day on them, particularly during the peak of the territorial season. They leave only if food or other requirements are not met on the area or possibly for dawn and dusk courtship flights, which in either case would be only for a

few minutes.

Certain areas within territories get more intensive use than others. In over half the territories favorite feeding and lookout points were determined. Male birds, and occasionally their mates, would pick certain locations among rocks where they would commonly rest for periods of fifteen to forty minutes at regular intervals during the day. The same daytime resting locations were probably used as night roosts. Only once was a bird observed after dark and he was in a location used during the day. In addition, the resting locations of males were usually in a position with good visibility over at least part of the territory. In three areas there were prominent rocks which overlooked at least half of the area. The rocks were used occasionally by males; once a male flew to his "lookout rock" to scream an answer to a rival's call. Intensively used feeding areas were those which had the most moist, young vegetation, but the vegetation was not analyzed in detail. On some territories these feeding areas change much more often than on territories which have more permanent moisture sources.

MATING BEHAVIOR

Formation of the Pair

Mating appears to have two main preliminary activities, the dawn and dusk courtship flights and the visiting of territories by lone females. Although males usually establish territories, several pair of ptarmigan were observed establishing territories after they were already paired. This suggests that at least part of the population pairs without respect to territoriality, possibly as a result of courtship flights only. The courtship flights are discussed below with other mating displays.

Four lone females were observed visiting territories. Each of these four had distinctly different patterns of pairing with males. Three of these were observed visiting territories occupied by already paired males and subsequently were observed on other territories. I assume that certain attractions are present on territories in addition to the male which may cause females to visit these areas. Thus a lone female visiting a territory on which a female is already present may be merely a consequence of visiting the more suitable areas. On the other hand, perhaps the males which occupy these areas are more sexually attractive. I suggest that these occurrences are a function of both factors. Evidence for this is (1) the instances of polygamy or second mating listed below; (2) larger number of female visits and pairings on certain large, early-established territories; and (3) one case in which a visiting pair of birds arrived near a well-established territory and the female left her companion to subsequently copulate and pair with the male of the territory after his original mate had nested. The original accompanying male

was not observed to be driven away by the resident male.

Two additional females were observed on different territories late in the season in what appeared to be a second pairing after loss of nests. One of these females was observed with her original mate for two days after her reappearance from nesting for a week. She had a well-defined brood patch at this time. Her old mate was beginning to act less aggressively by this time and was probably less sexually attractive, capable, or both. This female was seen on a nearby male's territory for part of one day and then paired with a male on a distant (one and one-half miles) territory where she remained for twelve days.

Selection of a mate, as suggested above, usually takes place early in the season through courtship flights and later through the visiting of occupied territories of either paired or unpaired males. However, formation of a pair occurs in some birds during courtship flights and no territory is subsequently visited and possibly the reverse situation occurs. Thus insufficient information is available to determine the relative importance of courtship flights, territoriality, and a combination of the two in pair formation.

The reasons for the selection of a particular bird as a mate by a female are difficult to discern. Courtship flights probably start in May. In the later stages of pairing and territoriality which were observed, more females frequented territories which were large and contained a combination of permanent water and other "preferred" habitat factors (see page 37). In addition, the males occupying these areas appeared somewhat dominant but were also probably those nearest the peak of breeding condition. The female actually paired with a male may be the first one who accepts him and thus produces a situation of mutual attraction.

The Pair Bond

Four pairs were observed for periods of over ten days and an average of eight observations were made on each pair (see Table VIII). In these four cases the pair bond was of great strength. Neither member of the pair was observed with another ptarmigan during the period and rarely were the birds over fifteen feet apart.

Defense of the female was clearly shown by all four males. Twice other males were driven away from the territories and the male returned to the female's side with a call which seemed to strengthen the bond, the pair remaining close together for some time after. When I approached a pair, the male almost invariably would make himself conspicuous first by standing up, craning the neck and flicking the tail in typical action which I have termed the "annoyance reaction" and which is often accompanied by a vibrant low clucking. The male rarely moved far from his mate, even when pushed, and often seemed to try to keep between the observer and the female. Once when both members of the pair were disturbed at a time when the female was beginning to nest, the male showed such a strong defense that I had to push him out of the way with a stick or my foot in order to follow the retreating female. These indications of a strong pair bond, at least in pairs occupying territories, are in keeping with the few published observations on paired White-tailed Ptarmigan (Packard, 1945; Bradbury, 1915) and certain observations on the rock ptarmigan (Bent, 1932).

The four pairs of ptarmigan observed for these long periods all performed almost every activity together. None of these were observed continuously from dawn to dusk, but long periods of observation indicated

their doing practically everything together and usually at the same time. For example, one pair was watched for seven continuous hours during which feeding and resting periods corresponded closely. When one bird moved in a particular direction for over a few feet the other soon followed.

Certain responses (other than the defense mentioned above and the displays below) between the two members of the pair were observed but not often enough to determine that they were unique to paired birds. These are a low cluck indicating a good source of food (apparently not the same as that used by the hen in teaching the chicks to feed), a clucking given at the approach of an enemy, and a sort of squawk given by the hen defending her nest from another hen (see Page 58) which induced immediate assistance from the male in driving the other bird away. In the latter action, the male did not respond negatively to the other female until hearing his mate call or hearing the associated sound of conflict between the two females.

Duration of Pairing

Table VI shows records of five males (including the four discussed above) observed to be mated to hens for periods ranging from three to eighteen days, the average period being over twelve days. In the case of the short period, the male may have been paired much longer beforehand and probably would have remained so longer afterward had not his mate been killed on the third observation day. She was ready to lay eggs at this time. This same male had another female with him at the time of his mate's death, but the second female did not remain in the area. In the five cases the end of the period of pairing came either when the female left

the territory or was killed, or when she began incubating eggs and thus was also no longer able to accompany the male.

TABLE VIII. Pairing of ptarmigan on territories at Logan Pass

Territory	Male	Female	Observations	Period	Remarks
1	511	505	8	16 day	
3,9	503	504	3,4	8 + 10	nest destroyed
7	513	517	2	3 day	female killed
8	516	504	6	12 day	
12	510	521	9	12 day	
AVERAGE			8	12	

Following the end of pairing, some males left their territory immediately, but some maintained it for a short time longer without, however, obtaining another mate. Two males were able to prolong their territoriality with a second mate.

In another case, two females and the resident male of a territory were within six feet of each other when first observed. There appeared to be no conflict between the two females although they were observed together for only a few minutes.

In one other case a male was observed to copulate with two different females within a few minutes. The second female had been aggressively pursued only minutes earlier by the same male in assisting his mate to defend her nest. This illustrates well the stimulus-triggered pattern of behavior common to birds. It was obvious that the male immediately

dropped the aggressive behavior in subsequent sexual excitement. Both before and after the brief mating display shown toward the new female the male either ignored or was aggressive toward her. This case should be considered polygamy, particulary since a few days later, after the first female was incubating, the male accepted the second female as another mate.

In three cases females were seen visiting territories of different males for long enough periods that mating probably took place. It is concluded, therefore, that ptarmigan have a pair bond which is strong for grouse, but in some cases are not monogamous in their mating relations.

Mating Displays

Calls. One distinct call, made by the male ptarmigan, seems to be primarily associated with mating. The call is scream-like and hard to distinguish from the aggressive scream of one male toward another. This scream-call was heard numerous times on the morning and evening flights and also was heard in the one instance of a location flight described below. This is undoubtedly the same call described as a "courtship cackle" by Packard (1945). If it is really the same as the defense-aggression scream, then it also is the same call he describes as a "series of raucous little screams." Weeden (MS) describes it as a scream and states that it is distinct from the courtship calls of the other two species of North American ptarmigan.

Another call distinctly associated with mating was heard in the few instances of observed copulation. Both the male and the female were quivering and excited at this time. The female gave constant, rapid calls which had a "squeaking" nature because of their high pitch and low

volume. The male answered this with a rapid "Brrrr" which was faster than her call, but also of low intensity. The latter sound is distinct from the rapid clucking of annoyance. The low, "squeaking" call of the female, however, may not be distinct from a more drawn out call she gives when approaching her nest and eggs.

Flights. Two special flight patterns appear to be associated with the mating of White-tailed Ptarmigan. The first occurs primarily in the very early morning and late evening when there is little light in the sky. This flight was observed or heard throughout the study period but was most intense during the territorial and nesting periods.

Crepuscular flights have been mentioned by Bradbury (1915) and Weeden (MS) but only the latter identifies these as courtship performances. However, Weeden indicated that these flights are taken by males pursuing one another and that females were never seen (by him) in courtship groups. Observations at Logan Pass indicate that males pursue females in at least part of these flights. Because of the low light levels and usually great distances from performing birds, sex of the performers was undetermined in all but four instances. Two of these four flights involved two males, and two involved a male and a female. Two birds seemed to be commonly involved in a single flight, but at least three took part in one, and a lone bird was once observed making a flight at dusk.

The general activity in dusk flights appeared similar regardless of the sex or number of participants, although more aggressiveness seemed to be present in flights where one male pursued another. The ptarmigan fly suddenly from a standing position, giving one or more screams in the

takeoff. The flight is low and erratic, covering distances as great as one-half mile. Very excited cocks will scream several times in flight and act aggressively toward the other male, including running pursuit on the ground after landing. Several flights may be taken in succession, not necessarily by the same pair of birds.

— In both cases where a male pursued a female the cock did all the screaming and pursuit on the ground. No strutting or other mating display was noted associated with these pursuits, although the male did not appear to chase the female with aggressiveness. The female would run short distances when the male got close, each time stopping or hesitating until the male caught up. Finally she would fly, with the male in screaming pursuit, presumably to land and repeat the process elsewhere. It could not be determined whether or not these courtship pursuits are followed by strutting and copulation as in the case of at least some of the rock ptarmigan (Bent, 1932).

— The second courtship flight was observed only once and may not be a common occurrence. This flight was a spiralling, vertical flight from a fixed location on a territory and resembled closely those described for certain rock ptarmigan by Bent (1932). The male flew straight upward, hovered for a second, screamed, then descended in a glide with a single spiral, landing with another scream and a series of clucks on a boulder about thirty-five feet from the starting point. The releasing stimulus for this display appeared to be the pinning of the female under a long-handled net for banding purposes. This unusual releasing sequence somewhat resembles the rock ptarmigan mating displays released by the killing of the female described by Hohn (1957).

Strutting. The display given by the male ptarmigan immediately prior to copulation I have termed strutting because of its similarity to the display of that name given by some other grouse. This display was observed only twice during the territorial and nesting period, once toward a female in the process of laying an egg and once toward a strange female (not the male's mate).

Two or possibly three separate sequences make up the strutting behavior. The first consists of short runs in pursuit of the female which avoids the male's approaches somewhat as described above during the crepuscular flights. Next the male stretches out his neck toward the female and swings his neck and body rapidly in a horizontal arc of about sixty degrees. This rapid swinging is done with a stiff body, pivoting mainly from the feet. This neck and body swinging action was not observed preceding a few other instances of copulation and may not be a sequentially-linked display.

The third sequence was a true strutting resembling that performed by a number of other grouse. The male holds his wings out to the side of his body, partially drooped and spread, occasionally dragging the ground. The tail is held almost vertically and fully fanned out. The red combs over the eyes are swollen and conspicuous. In this position, with neck stretched out toward the female, the cock makes short rushes at the female with very rapid, short footsteps. The female seemed less concerned by these rushes than the previous ones (in the first sequence) and shortly thereafter allowed the male to mount and copulate. During this last strutting both birds uttered low calls in rapid succession. These calls by the female were the only observed different action by her and

may have been the releasing stimulus for the strutting by the male.

Copulation. Copulation between White-tailed Ptarmigan was observed seven times, but only two different females were involved. In each case the pattern was the same. Both birds were excited and quivering, uttering rapid, low calls. In five of the cases copulation was not preceded by strutting. The stimulus for copulation apparently was the female on the nest in the process of laying an egg, or sounds made by her at this time. I suggest that the copulation stimulus is a combination of a call and the female in a crouched position. At certain moments the male would rapidly approach the female and copulation would occur on the nest, but the call, if present, was not clearly distinct from the low calls given by the female in the laying process. When the male copulated with the female off the nest, the action was preceded by strutting displays including short pursuits, the female accepting the male in a partial crouch at the time of copulation.

Copulation itself was very brief, lasting from ten to thirty seconds, but being repeated at least twice in the observed cases. Both birds were quivering and excited during the whole performance; the whole body quivered and rapid, low calls were given. The female crouched with her wings and tail partially spread and the male stood on the female's back with widely spread wings drooping and fluttering slightly. Then the male backed down and lowered himself until their tail feathers touch; presumably the cloacal regions were in apposition at this time. No special motion other than the general vibration was noted. The male then quickly stepped off, leaving the female in the crouched position, usually with her throat palpitating. One male copulated with two

different females, each in plain sight of the other, but the lone female appeared indifferent in both cases.

Post-copulation. At the termination of copulation both sexes are excited and their throats palpitate in a "panting" action. The male exhibits a special activity after copulating five or six times which I call a post-copulation display. He would seize twigs, moss, or anything handy and then extend his head and neck over his back and drop the object. These objects would strike the back or side just behind the wing and drop to the ground, or some would momentarily rest at the base of the tail. This action continued for several minutes and was briefly repeated twice thereafter, appearing to me to be an attempt to contact the stimulated cloacal region. No such action was exhibited by the females.

NESTS

Nest Territory and Nest Site

The variety of ptarmigan nest sites reported in the literature (Bailey, 1921; Bradbury, 1915; Davies, 1889; Dawson, 1909; Lewis, 1904; Sclater, 1912; Swarth, 1935; Taylor, 1920; Weydemeyer, 1931) indicates little in the way of common characteristics. All authors agree that some form of nest is built on the ground above timberline. Most feel that the nest is in the open, not covered by tall vegetation or under rocks, although many mention rockiness and low plants such as grass or heather on the site. There is little agreement or even mention of slope, aspect, soil moisture, and specific mode of construction.

All of the authors describing nest sites (above) and many others (Bailey, 1928; Booth, 1950; Gabrielson, 1959; Headstrom, 1951; Hoffmann, 1927; Jewett, 1953; Macoun, 1909; Pearson, 1936; Pough, 1957; Racey, 1948; Raine, 1892) have varying and conflicting descriptions of the nests themselves. Gabrielson and Pearson come closest to the observed variation in stating that the nest varies from a simple depression in the ground to a carefully made and elaborately lined structure.

Only three nests were found on the Logan Pass study area in 1959. None of the three was on the territory of male birds, and may instead have been located on specific nest territories. One female defended only about a two-foot radius around the nest against another female, although the male extended this area by ten feet when he temporarily assisted in the defense. The only other defense of nest territory observed was when a male consistently stayed between the observer and the nesting female

and had to be pushed out of the way to approach closer than about ten feet to the female and the nest.

The characteristics of the three nest sites are categorized into rock, water source, exposure, and plant association. Each category will be considered separately in order to compare the three sites.

The first nest was located on the flat of a small ledge with a moderate amount of loose rock along one border. The second nest was located on the flat top of a broader, more vegetated ledge that had little loose rock. The third nest was located under the edge of a boulder in a large open area that had moderate amounts of loose rock, especially of boulder size.

No permanent water source was present on the first nest site. However, the ledge had only been snow-free about three days when nesting began and the surrounding banks kept the area moist for over three weeks. The second nest site was the most moist, having been snow-free only a day when nesting began and being vegetated heavily with water-retaining mosses. A small rivulet about ten feet from the nest ran throughout the incubation period. The third nest was on the driest site, which was rocky and well drained. No permanent water source was nearby, but the surrounding snowbanks kept the site moist throughout the nesting period.

The first nest was sheltered somewhat from wind and rain by the overhanging branch of an Engelmann spruce. The nest was exposed primarily on the east side so that the same vegetation gave protection from the hottest sun. The second nest was in a rather exposed site at least for the first two weeks of incubation. There was no overhead cover to protect from storms and excess sun. However, this nest was located beside some small willows which had leafed out and gave some wind and

sun protection during the later parts of incubation. The third nest was under partial overhead rock cover and faced northwest. It therefore had some protection from rain, prevailing winds (in that site) and strong sunlight.

The first nest was located in a bed of heather. The surrounding vegetation was primarily a dry ledge type with some krummholz. The second nest was located in mosses and grasses among scattered willows averaging twelve to eighteen inches high. The remainder of the ledge was primarily a wet ledge association. The third nest was located in an area of sparse grasses and herbaceous plants. It may be considered a dry ledge association although it had some of the characteristics of a fell-field type.

Despite their differences, certain characteristics were common to the three sites.—Nest sites found on this area by Evans and Fisher in 1958 (MS) also have these same common characteristics: (1) nests are near to, on, or under rocks of various sizes; (2) nests are in newly snow-free sites and generally near to snow or some other water source; (3) nests are in or near to preferred food sources; (4) nests (and the nesting hen) are inconspicuous by color, cover, or both; (5) nests are generally protected from excesses of sun, wind, and sometimes storm flooding.

Site Selection

Insufficient data were gathered to determine clearly the factors involved in the selection of the nest site. Two females were observed almost daily during the period in which they picked a nest site and constructed a nest. Both of these females selected a site off their mate's territory after apparently visiting, with the male in company, a number of potential sites both off and on the territory.

These females apparently did not select the final nest site before the day on which the first egg was laid and they continued to improve the nest during the laying period rather than beforehand.

The phenological stage of an area seems to play a role in its selection. Each nest site had not been free of snow more than a few days and consequently remained moist throughout the incubation period. The 1958 nests seemed to be concentrated along permanent water sources which would meet the same requirements during such a relatively dry year.

Nest Construction

Two authors (Dawson, 1909; Jewett, 1953), both referring to the White-tailed Ptarmigan in Washington, state that the female excavates a depression in the ground and lines it with vegetation. No other authors describe the building process. Actual building was not observed at Logan Pass, but none of the three nests had been excavated in the ground. The first was a shallow, hollowed spot in a heather-bed, the second a deeper hollow in mosses, and the third a nest of grasses built up from the ground.

The three nests found at Logan Pass in 1959 varied greatly in structure as well as location. Nests found the previous year by Evans and Fisher varied similarly, but no measurements are available. The first nest had inside dimensions of 100 x 110 mm. and was 35 mm. deep. Materials consisted of dry grass and a few feathers lining a hollow in heather.

The second nest was more oval and deeper, measuring 100 x 120 mm. x 60 mm. The outside dimensions were approximately 180 x 190 mm. This nest was made of interwoven grasses forming a thick lining around a hollow

in the mosses underneath. About a fourth of the nest's total depth was above the level of the surrounding mosses and this portion had some feathers incorporated into it.

The third nest was circular with an inside diameter of 100 mm., and outside diameter of 150 mm. and a depth of 50 mm. This nest was built of grasses poorly woven and piled on bare ground under the overhang of a boulder.

The first two nests were observed during laying and they were added to or deepened somewhat over this period before incubation. In the one observed instance of laying, the female rearranged some of the grasses lining the nest and left more feathers in it at the end of the laying process.

It was not determined whether the male participated in nest construction. However, only once did a male show interest in the nest. In this instance the male stepped over the nest, stopped, pecked at the eggs, momentarily settled on them, then immediately rose and left.

Laying

No published reports on White-tailed Ptarmigan include description of the laying process and only one author (Bradbury, 1915) incompletely describes the laying interval for two hens. During the 1959 study, two females were observed during the laying period as they completed their clutches.

Time. Female number 505 had laid four eggs by June 28, while female 521 had laid four by July 7. This difference in actual date is probably unimportant, as the females were paired with males beforehand for thirteen and nine days respectively and the nesting areas had been free of snow six and four days respectively and thus were phenologically similar.

Eggs were not laid at a particular time of day. Table VII shows known layings at noon, in the afternoon, and at night.

Interval. There is no regular interval between successive eggs, but approximately thirty hours appears to be average (Table IX). The final egg was laid after a somewhat longer than usual interval and in these cases after incubation had commenced.

TABLE IX. History of the eggs in two ptarmigan nests at Logan Pass

Egg	Female No.	Date and Time Laid	Size in mm.	Hatch Date and Time	Remarks
1	505	By 6/28 noon	30 x 40	pipped 7/23 noon	out and dry (chicks) 6 A.M. 7/24
2			29 x 38	same	same
3			29 x 42	same	same
4			31 x 45	same	same
5		6/28 3:30-5:30 P.M.	28 x 41	same	same
6	"	6 P.M. 6/29 to 2 P. M. 6/30	29 x 39	pipped 7/22 1 P.M.	hole 7/23 P.M.
7	519	same	29 x 40	failed	incubation begins
8	505	7/1 12:30 P.M.	29 x 41	near noon 7/24	observed laying
9		4 P.M.7/2-5 P.M.7/3	27 x 38	premature 7/24 crack 6 P.M. out 11 P.M.	died 7/25
1			30 x 43		
2			28 x 43	incubated through 7/22	eggs disappeared
3	521	by 7/7 4 P.M.	29 x 42		
4			29 x 43		
5		5:30 P.M. 7/8-5:30 A.M. 7/9	27 x 38		

Laying behavior. One female was observed in the process of laying an egg. This bird returned from the male's territory to the nest and settled on the previously laid eggs with low, "squeaking" calls. Within fifteen minutes she was restless, "panted" some and readjusted herself several times on the nest. Then the male of the pair, who was within fifteen feet of the nest during this time, came over and copulated briefly with the female on the nest. The releasing stimulus for this action was not observed. The female after this appeared more excited and "panted" a great deal, occasionally giving muted, low calls. Soon she was half standing in the nest, slightly quivering, and the male again came to the nest and copulated with her. This same sequence was repeated once more. The female now had her beak open, panting heavily. She then raised her tail a bit and deposited the egg from a half standing position. After about ten seconds she settled back on the eggs, again panting and giving sound. Soon she raised up and turned around in the nest, readjusted the eggs and settled down. At this point the male again returned and copulated with her two more times, each time leaving the female with her feathers somewhat puffed up and panting. After a rest period of about twenty minutes she left the nest and fed for fifteen minutes, after which she returned to the eggs to begin incubation. During the subsequent twenty-three days she was never observed off the nest.

Clutch

Size. The two clutches observed were nine and five eggs respectively, and the first one may have been contributed to by two females.

Various authors report numbers of eggs varying from three to sixteen (Bailey, 1921, 1928; Booth, 1950; Bradbury, 1915; Davie, 1889; Gabrielson, 1959; Grosvenor, 1937; Hoffmann, 1927; Jewett, 1953; Lewis, 1904; Maynard, 1890; Pearson, 1936; Pough, 1957; Raine, 1892; Sclater, 1912; Weydemeyer, 1931), with some authors stating ten to sixteen as typical for the species. There seems to be no justification for these high figures. The eighteen clutches described in the literature contain from four to eight eggs with one clutch of ten. The average size of these reported clutches is 5.7. Five Logan Pass clutches (including three from 1958 found by Evans and Fisher) range from three to nine eggs with the large clutch possibly contributed to by two females. The average size of these clutches is 5.2 eggs.

Description. Table VII presents the dimensions of the fourteen eggs found in 1959. The final egg laid by each female was the smallest in the clutch. The eggs vary in color and amount of spotting, but generally are buff, speckled lightly with dark brown.

Incubation

Duration and periodicity. Incubation began three days (two eggs) before the clutch was complete in nest one and the last two eggs consequently hatched after the other chicks had left the nest. This early incubation may have been a result of competition for the nest with another hen. In the second nest incubation also began before the last egg was laid, but hatching was not observed for sequence correlation. Incubation lasted almost exactly twenty-four days in the case of the first nest. The second nest was destroyed after sixteen or seventeen days of incubation.

The two hens were rarely observed off the nest. Hen 505 was observed one to three times per day on twenty-two of the twenty-four incubation days. In approximately fifty observation-hours she was always incubating on nest one. During the entire incubation period she was only reported off the nest once, and this was a dusk observation by another observer. Hen 521 was observed on fourteen of the sixteen days of incubation before the nest was destroyed, sometimes several times per day. In approximately thirty observation-hours she was only observed off the nest once and this was during the second day of incubation. At this time she was off the nest for twenty minutes and ventured up to thirty feet away, feeding heavily. The temperature was fifty-five degrees at 3 P. M. of a sunny afternoon, so the temperature of the eggs was probably maintained. During the following two weeks of observation the only evidence of the female leaving the nest was clocker droppings at a pool of water five feet from the nest.

The weights of the hens, while taken only twice, indicate a loss during incubation, probably due to the restricted amount of feeding since they rarely left the nest. Hen 505 weighed 370 grams fourteen days before incubation and 333 grams on the last day of the twenty-four day incubation period. A loss of at least 37 grams is indicated or about 1.6 grams per day of incubation. Hen 521 weighed 410 grams eight days before incubation and 380 grams after fourteen days of incubation. The indicated loss of thirty grams or over two grams per day may be somewhat biased by the additional weight of forming eggs at the time of initial measurement.

Both females refused to leave the nest after about the third day of incubation and had to be pushed aside to view the eggs. When removed

from the nest during the laying period, female 505 fed before returning to the nest, but during the incubation period she always returned immediately. Female 521 always returned immediately without feeding when removed from the nest during the incubation period. When weighed on the fourteenth day, for example, she was thoroughly handled, yet when released she walked only six feet away, hissed, flicked her tail and gave disturbed "churrs." As soon as I moved six feet from the nest she returned within thirty seconds to the eggs without pausing for food.

Behavior of hens. Both incubating females remained on the nest through all kinds of disturbance by man and inclement weather. Loud and strange sounds, sudden and threatening movements, and physical disturbances, such as pushing or stroking, usually only evoked alertness or a hissing and pecking response from the hen. The latter response was usually directed toward a hand reaching under her into the nest.

Both hens were observed to sit quietly through hail and rain storms of considerable force which probably would have destroyed the nest if the females had left. Violent winds, up to thirty miles per hour at five feet off the ground, and thunderstorms did not disturb these females. Very calm, warm weather probably was harder on the females than were storms. The females are heavily feathered, with fairly dark plumage, and appeared to become overheated readily on sunny days. At these times the ptarmigan did not move or ruffle their feathers, but maintained the same position on the nest with their beaks open and throats palpitating rapidly. Some cover was present either above or to the side of all but three of fifteen nests found at Logan Pass in 1958 and 1959. This cover may provide shade during at least part of the day and help prevent

over-heating of the incubating hens.

No specific pattern of entering and leaving the nest was noted, although the two hens generally faced into the wind and away from the sun. Two nests were slightly oval in shape with an approximate north-south axis so that the hens faced either north or south.

A hen usually arranged the eggs with her beak, tucking an out-of-place one under her toward the rear. She would then settle to the clutch with a rocking, side-to-side movement which became more rapid as she settled further down. During the laying period females were observed off the nest three times and each time the eggs had been lightly covered with vegetation.

Both females had large incubation patches devoid of feathers, as did all females with young broods. The hens apparently pluck these feathers during the laying period and some of them are used in nest construction. This large patch was useful for identification of birds which were or had been incubating, at least until full feather re-growth, which was completed at least a month after incubation.

The males appeared to take no part in the incubation and care of the young, although they were attendant during laying. One observation indicated interest in the eggs by the male. Not long after copulation a male stepped close to a nest of seven eggs which the female had momentarily vacated. The bird looked into the nest, then pecked at it and the eggs. He next stepped forward and sat down on the eggs for a very few seconds, getting up immediately and leaving the site.

The fidelity of the hen is in keeping with observations by several authors (Bailey, 1928; Bradbury, 1915; Dawson, 1909; Lewis, 1904; Swarth, 1935; Taylor, 1920; Weydemeyer, 1931), but is definitely

not a matter of being "used to" handling as suggested by Swarth (1935). The hissing and pecking response to touching was also observed by Bradbury (1915), Dawson (1909), Lewis (1904), and Weydemeyer (1931). Although one author (Terres, 1958) reports a hen incubating under newly fallen snow and another reports a hen in a partly flooded nest (Bradbury, 1915), there are few published reports of weather effects on nesting ptarmigan. Evans and Fisher's work indicates flooding as a major factor in destroying ptarmigan nests in 1958 but this was not the case in 1959.

Hatching

Time. Table VII shows the hatching date and time for one brood of ptarmigan. The second clutch of eggs was destroyed, but would have hatched one week later if the incubation period of twenty-four days is constant. Those eggs (#1, 6) in the first clutch which were incubated for the same length of time all hatched during the night of July 23-24, and the chicks were dry by the following morning. The one egg farthest advanced (hatching earliest) was the one laid on the day incubation began (#6), thus not needing a re-warming period before continuing development.

The brood table (Table X) shows the estimated ages of the twelve broods found at Logan Pass. From this information, and the two known age clutches above, the hatching period in 1959 appears to have been between July 16 and 25.

Process. Apparently no author has described the hatching process in White-tailed Ptarmigan. The clutch of nine eggs in Table VII was observed during the hatching process and two eggs were observed continually during the actual emergence of the chick. At the end of twenty-one days of incubation (July 21), no sound came from within any egg. At twenty-one and one-half days, one of the six eggs which hatched together began audible pipping. By twenty-two days, three of the six eggs had begun to pip. Six hours later, a small crack was visible in the shell of the most advanced egg (#6). Loud pipping sounds came from

TABLE X. History of broods observed at Logan Pass in 1959

Brood, Female	Chick No.	Est. Hatch	Observation Dates*	Mortality	Remarks
1	45	7/20	7/23,27 9/14,15		two chicks in brood
541	46		same		on 9/19,20,21.
	47		same		early mortality
	41½		7/23	1	
2	48	7/23	7/24,29 8/29 9/3,16		
502	49		same		
	50		same		
	51		same		
	2½		7/24	1	early mortality
3	627	7/24	7/24,25,27,8/26,9/1,		reduced from 4 to
505	628	1-5 A.M.	9/6,11,13,16.		3 about 9/5
	629		7/24,25,27,8/26,9/1,		
	630		9/6,11,13,16.		
	5a		7/24,25,27	3	
	5b	"	same	or	
	5c	1 P.M.	same	4	½ day younger
4	52	7/23	7/26,30 8/14,18,19,		two chicks in brood
542	53		8/21,28,29, 9/12,14.		on 9/19
	54		same plus 9/22		
	42½		7/26	1	early mortality
5-543	44	7/22	7/27,9/7,15.	0	
6	57	7/24	7/31,8/29,9/11,12,13.		with brood 3 on
556	58		7/31,8/29,9/11,12,14.		9/13
	59		7/31 8/29	1	killed 8/29
7	60	7/17	8/1, 11	0?	
563	61		same		
	62		same		
8	65	7/19	8/2		
570	66		same	?	
	67		same		
	68		same		
	69		same		
9	76	7/21	8/7	2	
575	77		same		
	78		8/7,26 9/15		
	79	7/17?	same		adopted?

TABLE X (continued)

Brood Female	Chick No.	Est. Hatch	Observation Dates*	Mortality	Remarks
10	84	7/17	8/7		
583	85		same		
	86		same	?	
	87		same		
11	93	7/20	8/11,17, 9/1,11,14, 9/15,23.		3 in brood on 9/16
597	94				
	95		8/11,17 9/1,11,14 9/15	0?	2 in brood on 9/23
	96				
12	98	7/24	8/13,17,28,29 9/19,22		
600	99		8/13,17,28,29 9/19,22	0	
AVG.	4 ea.	7/21	5 observations each	30%	46 total ind.

*__Date when measurements were taken (see Table XI)

TABLE XI. Measurements of broods observed at Logan Pass

Chick No.	Foot Length in mm.	Total Length in mm.	Weight in Grams
45	34,42	96,115	nt* 27
46	38,43	92,121	nt, 27
47	39,46	94,123	nt, 27
41½	39	93	nt
48	38,42	96,112	13.5, 27
49	38,43	91,121	13.5, 27
50	38,42	94,119	13.5, 27
51	39,42	93,119	13.5, 27
2½	39	95	13.5
627	40,43,66,70	91,96,255,295	13,16.5,190,250
628	37,40,67,70	90,97,255,296	13,16.5,195,253
629	40,41,68	92,98,255	13,16.5,203
630	39,41,67	92,96,236	13,16.5,155
5a	38,40	91,98	13,16.5
5b	38,40	92,101	13,16.5
5c	36,40	85,91	12,16.5
52	40,44,60,67	101,125,235,255	20,30,147,203
53	39,44,64,69	98,124,240,260	20,30,150,215
54	40,44,60,68,69	98,123,234,265,295	20,30,145,205,321
42½	40	97	20
44	42	103	23
57	44,70,73	126,274,300	29,217,282
58	44,68	121,273	29,210
59	45,70	125,263	26,206
60	53	166	59
61	52	172	59
62	51	173	
65	51	160	54
66	47	150	54
67	49	152	45
68	48	155	48
69	48	150	47
76	nt	172	60
77	nt	204	73
78	nt,68	194,260	75,193
79	nt,72	236,285	104,233

TABLE XI (continued)

Chick No.	Foot Length in mm.	Total Length in mm.	Weight in Grams
84	64	215	127
85	62	205	112
86	64	215	116
87	64	215	120
93	68,74,76	220,300,315	135,281,342
94	69,76,77	218,294,310	130,270,349
95	65,75	212,282	131,257
96	66,75	215,290	134,270
98	60,70,74	210,275,310	120,225,365
99	53,68	190,260	110,185

*nt - not taken

within the other two, and weak tapping sounds indicating the beginning of pipping came from the remaining three.

Initially, the interval between tapping sounds was about twenty seconds with rarely over three or four taps in a group. Just prior to cracking of the shell, tapping sounds were louder, in groups up to ten pecks each, and often with less than ten seconds pause between groups. All six eggs were cracked at the beginning of the twenty-third day and faint peeping from the chick inside the most advanced egg could be heard. Four hours later the two other slightly more advanced chicks (#2 and 3) were beginning to make peeping calls from within the egg. The most advanced chick (#6) was now calling loudly enough to be heard six inches from the egg and the hen began to answer these calls with drawn out clucking calls. This same chick succeeded in breaking loose a small piece of shell within two more hours, and one hour later, broke through the shell membrane at this point, making an open hole about one-eighth inch in diameter. This first opening in the shell, through which the egg tooth on the beak of the chick could be seen, was made approximately twenty-four days after the egg was laid and in this case twenty-three and one-half days after incubation began. Within the next eight hours the remaining five chicks broke holes through their shells and completed emergence so that all six chicks were out and dry twenty-four days after the beginning of incubation. One egg was hatched artificially and another naturally after the first group of six had hatched and left the nest. In the former case, the egg had been cracked prematurely by accident although the chick had begun to tap at the shell by himself. This chick took five hours to get out of the cracked shell. It was kept at a temperature of about ninety degrees during this time by the heat of

a Coleman gas lantern. A very small bulge of yolk was visible on its abdomen at the time of hatching and it was nearly gone eight hours later. This chick was born about two days prematurely.

The other chick which hatched after the brood left the nest emerged by itself twenty-three days after the egg was laid. Incubation had been in progress one day when this egg was laid; therefore, twenty-three days represent the minimum incubation period. It took about four hours from the time the initial hole was made for this chick to get out of the shell.

Both chicks were observed to emerge by the use of two movements in addition to the pipping of the shell by movements of the beak. When still in the shell, some twisting movement was shown which turned the chick slightly within the shell. This turning appears to make more shell available to either side of the initial hole for lateral widening. Only slight lateral widening was actually observed, but broken shells from emerged chicks appeared to have been chipped laterally along the breakage plane for about one-quarter of the circumference of the egg. The final emergence was accomplished in both cases by a straightening action of the chick's body. Continual attempts to straighten the curvature of the back and neck resulted in pressure against the ends of the egg which opened the crack formed by the beak in much the same manner as one opens a hen's egg to fry it. In the case of all eggs, two pieces remained in the nest after hatching. The breaking plane was transverse and located approximately two-thirds of the length of the egg. Bloody fetal membranes are visible in these "half shells" for weeks after hatching and probably would serve to distinguish these shells of eggs broken by predation (at least up to a week before hatching) throughout the season in which they were laid.

The hen led the newly hatched chicks away from the nest within twelve hours, probably about eight hours, of the time they emerged from the shell. The unhatched eggs and shell remains were left in the nest. These unhatched eggs were found by the author in time to hatch one artificially and rescue the other one from which the chick was emerging; but under natural conditions these abandoned chicks undoubtedly do not survive.

Young Chicks

Description. Thirteen one- and two-day-old chicks were observed. The hatching date within a few hours is known for eight of these. A single chick was hatched prematurely and its measurements taken within twenty-four hours so that they represent the size of a chick at birth or a few hours before. Table XII shows the measurements of the thirteen newborn chicks.

TABLE XII. Comparative measurements of chicks two days old or less

No.	Age in Days	Weight in Grams	Total Length in mm.	Wing	Foot	Width of Skull in mm.	Length of Beak	Tail	Remiges in mm.	Remarks
1	0	11	83	25	34	12	6	none	none	premature
1	1	12	85	28	36	13	6	none	5	balance poor
6	1½	13	91.3	34.3	38.3	14	7	none	8	run fair
5	2	13.5	93.7	32.0	38.5	14	9	none	10	run well

The two chicks which were measured for the zero and one day ages had done practically no feeding or exercising, so that their measurements

may be somewhat smaller than those of nest-hatched chicks of the same age. The remaining six known-age chicks fall in the day-and-a-half age class. Their weights were identical within the limits of the scale used, and their total length only varied one millimeter. Wing length from the axilla to the end of the carpals varied one half millimeter and spread of the foot from front to back varied one millimeter. Width of the skull and length of the beak did not vary. No rectrices had appeared and remiges varied one millimeter from an average length of eight millimeters. The measurements of the five two-day-old chicks varied in the same order of magnitude.

The newborn chick is covered with natal down in a mottled tan and brown pattern, except for the wing primaries. The primary feather sheaths seem to appear just at birth or a little before and develop rapidly. The juvenal primary feathers begin to emerge from the sheath on the first day after hatching and protrude approximately ten millimeters on the second day. Sheaths of the rectrices, however, do not appear until about the sixth day. Length of the wings and feet increases rapidly during the first day of growth; the ability of the chicks to balance themselves and run shows a corresponding increase.

Behavior. A response bond between the hen and chick seems to be established even before hatching. Two chicks (numbers 8 and 9, Table IX) were hatched after the hen had left the nest with the remainder of the brood. These two chicks had pipped their shells and called from within them before the hen left the nest. When hatched out, these chicks showed no response toward me, although I was the first living thing they saw. The following day, I performed an experiment to see whether these chicks

would respond to ptarmigan other than their mother.

When the two chicks were placed near a hen which had not incubated, they gave loud calls. The hen showed little interest in them and did not reply with motherly calls. The chicks remained where they were although the hen was in plain sight. When these same chicks were placed near a male ptarmigan, the action was similar. However, this apparent lack of sight stimulus may be biased by the very young age (approximately one-half and three-quarters days) and weakness of the experimental chicks.

When these same two chicks were placed by their own mother a few hours later, she answered their calls. The chicks responded to her calls by trying to get to her side. The hen then came toward them and eventually brooded them. The evidence from these observations points to a chick-hen bond based on the sound of the motherly clucking of the hen established even before hatching rather than based on sight stimulus after hatching.

Day-old chicks were observed to feed on almost everything. Bailey (1918) has undoubtedly the most complete published observations on newborn White-tailed Ptarmigan. She observed chicks pecking at anthers of Dryas and dwarf willow among other grasses and flowers without any apparent direction on the part of the hen. Pickwell (1941) records browsing on succulent moss. Evans and Fisher (MS) apparently have made the first records of feeding intervals and specific foods used in quantities by newborn chicks. These authors mention feeding on insects and leaves of plants such as willow for fifteen to twenty minutes and then, with full crops, being brooded by the hen for a similar period of time. My observations on young chicks include cases similar to all of the above.

Day-old chicks at Logan Pass sampled seed heads, buds, flowers, insects, and some leaves. During the first day in particular, the

chicks would peck at anything conspicuous which they passed, including in some cases non-organic objects. This trial-and-error method was supplemented by teaching activity on the part of the hens (see Page 90). A moving insect was quickly chased by chicks and seemed to be a preferred food along with certain seeds, buds, and flowers. A discussion of chick food habits is beyond the scope of this paper. I suggest that these foods all have a natural high food value and are taken by the chick instinctively or discovered by chance. The day-old chick which had never seen its mother picked up these good foods in about fifty per cent of his feeding attempts. This natural use of high protein, concentrated foods parallels the observations by Gelting (1937).

Feeding activity during the first day lasted from fifteen to thirty minutes between resting periods. Brooding by the hen comprised only about half of these resting periods on the two days when observations were made. Since the weather was very warm and favorable during the observation period, actual brooding may not have been so necessary. When resting on their own, chicks would squat in shady spots in groups of two or three, sometimes for brief periods of only a few minutes rather than the longer periods taken when brooding. Resting or brooding periods became rapidly fewer and shorter. The last brooding was observed when chicks were about ten days old.

Newborn chicks relied mainly on their mother for danger warnings. A threatened chick, not pre-warned, would more often run than hide and peeped loudly when caught. Often if approached carefully they did not know they were in danger and even fed within a few feet of the observer. A natural curiosity was shown toward rocks, holes, snow, and water.

Chicks usually approached, rather than avoided these things.

Parental care of young chicks. In the single observed hatching the hen responded to calls of the chicks with low clucks as much as a full day before hatching. The hen apparently remained on the nest throughout hatching. In the initial observation on the hatching morning, one chick was in the nest underneath the hen and still wet; the remainder (5) were partially under her wings in a brood position.

Within seven hours of this initial observation at hatching, the hen led the chicks away from the nest.

For the next day she remained within 150 feet of the nest and stayed very close to her brood while they developed the ability to walk, run, feed, hide, etc. From the time the brood left the nest, the hen took part in teaching activities by being an example for the chicks either unconsciously or purposely. She was noticed walking slowly about during the entire first day, pausing to feed and let the chicks catch up, much as described by Bailey (1918). During this day the chicks were not observed over six feet from the hen and she brooded them every twenty to thirty minutes. A low call was noted which served to bring the chicks to her for brooding purposes. This moving and resting sequence may be important in the rapid acquisition of balance and walking ability during the first twenty-four hours of growth.

Eight different broods were observed whose chicks were under two weeks old and many of these broods with young chicks were re-observed numerous times. Hens in four of these broods were observed to teach the chicks to find and recognize certain foods. In one instance, a hen was feeding and found some new shoots just breaking the ground surface. After

clearing the area with her beak, she gave a call which brought all four of her three-day old chicks to the spot where she was pecking. Then she stepped back and three of the chicks pecked for a while in the same area. Similar cases were observed on slightly older chicks; for example, a hen found a group of Ranunculus flowers, just opening, called her chicks, and both parent and chicks consumed all of the flowers.

Teaching of self-preservation was not observed, but the parent gave certain calls at which the chicks immediately squatted and hid themselves. Progressive changes in the call and response were noticed. As they grew older and became more and more alert to dangers, the chicks began to move away from the parent into better hiding spots when warned. Chicks were first observed to hide or fly for escape on their own judgment at about two weeks of age. This tendency increased and watchfulness by the parent decreased as chicks grew older. Chicks were first observed to give their own warning calls at about five weeks of age. These calls are indistinguishable from those of the parent and were probably learned from them.

Hens protected their young from the weather by brooding and sheltering with the body for about the first two weeks of life. After this time, little brooding was observed, although hens occasionally stood over chicks to provide shade for them. It is doubtful that the hen protects the chicks through selection of certain locations. No significant difference in location of broods on the study area was noted between different periods of chick development. The slight differences shown could be more readily attributed to availability of moist, young vegetation than to protection from unfavorable weather or enemies. In some cases indifference to man's possible detrimental effects was clearly shown by certain

hens. Such hens and their chicks could be found for several days within a hundred yards of a location where they had been captured and banded.

All hens showed some degree of defensive response to the call of a distressed chick. The aggressive defense response was shown best in hens with young chicks but was still shown by some hens when the chicks were six weeks old or three-quarters grown. This response seems to be induced almost entirely by the loud peeping sounds of a distressed chick. The response is intensified by larger numbers of distress calls (e. g. from several captured chicks at once) and the sight of struggling chicks. The hen in full defense display exhibits fully spread wings and erect, spread tail. Short aggressive runs are made at the enemy with considerable hissing. In a few extreme displays, the hen pecked at the hands of the person holding the chicks and flew at his face and head.

These defense responses were shown best by hens which had none of their brood with them. Hens responded less to a lost chick or distressed chick calls when they had several chicks with them. Less violent responses, such as hissing or making themselves conspicuous, were exhibited by hens in cases where danger threatened the chicks, but no sound stimulus was involved.

The visual stimuli in the latter cases were all provided by man, but presumably enemies, particularly ground predators, would evoke these responses. Hens hissed when the observer got within a few feet of young chicks. When a person suddenly came upon a brood at close range so that the hen was startled, the chicks would usually hide immediately and the hen would run a few feet with white rectrices and remiges showing. This show of bright feathers effectively attracted attention to the hen who, if followed, would continue to move away from the brood in short runs.

While not a true "broken wing act," this distraction display served a similar purpose. Three hens were followed in such circumstances and each one stayed fairly close to the pursuer until they were one hundred to two hundred feet from the brood. In each case the hen disappeared from view once this distance was reached. In one case the hen had hidden herself behind low krummholz, while in another case the hen was observed sneaking slowly back to the area where the brood had been. In the third case the hen could not be located until she gave herself away by calling back to a lost chick. This latter response was capitalized upon thereafter when a hen could not be located. Over fifty per cent of lost-chick-peeping imitations by the observer netted a response from the hen. In some cases at this chick call a hen would appear on a prominent rock or come toward the observer.

The display, toward humans at least, seemed to be modified by the fear or other associations which the hen had with the enemy; for instance, a hen which had been caught, handled, and banded usually showed a markedly less violent defense response to calls from the distressed chicks than before she was handled. In addition, the hen which had been handled at the nest almost daily during incubation showed much less aggression toward the observer holding her chicks than did other hens.

In many cases it was clear that hens are not aware of the number in their brood. Experiments were made in eleven instances to see if hens recognized the number of individuals in their brood. Chicks were held and released one at a time to the hen and the number at which the hen considered her brood complete and moved them away from the threat was recorded. In only three of the eleven cases did the hen wait for her complete brood. Furthermore, all three of these cases were small broods of

three or four. One hen left when she had three of five and another when she had only four of seven chicks. The average females left when they had about seventy-five per cent of their brood back. Additional chicks were also accepted. A hen which had six chicks already with her was presented with two more. She responded immediately to their calls and took them under to brood with the rest. This lessened protective response, once the brood is seventy-five per cent complete, may be a significant factor in chick mortality.

Half-Grown Chicks

Body growth. Figure 5 shows the growth of chicks from birth to adult size. Growth of body size, as indicated by total length, is essentially linear and adult size is approximated at the end of six weeks. Weight increase follows a somewhat sigmoid curve, lagging behind body growth for two and one-half weeks, then increasing sharply for a week, and climbing steadily thereafter with a slight progressive decrease in rate. Adult weight is essentially reached at the end of eight weeks. The rapid growth shown between two and three weeks comes just after the juvenal plumage is essentially completed and is probably a function of the transfer of energy from feather growth to body growth.

This rapid growth rate is a distinct advantage to the ptarmigan which live in an environment with a very short summer season. In 1959, chicks probably hatched at least two weeks later than usual, about July 22, but nevertheless were adult size by mid-September, almost a month before winter snows became serious enough to close the Logan Pass highway.

Feather growth and change. Feather growth in young ptarmigan is

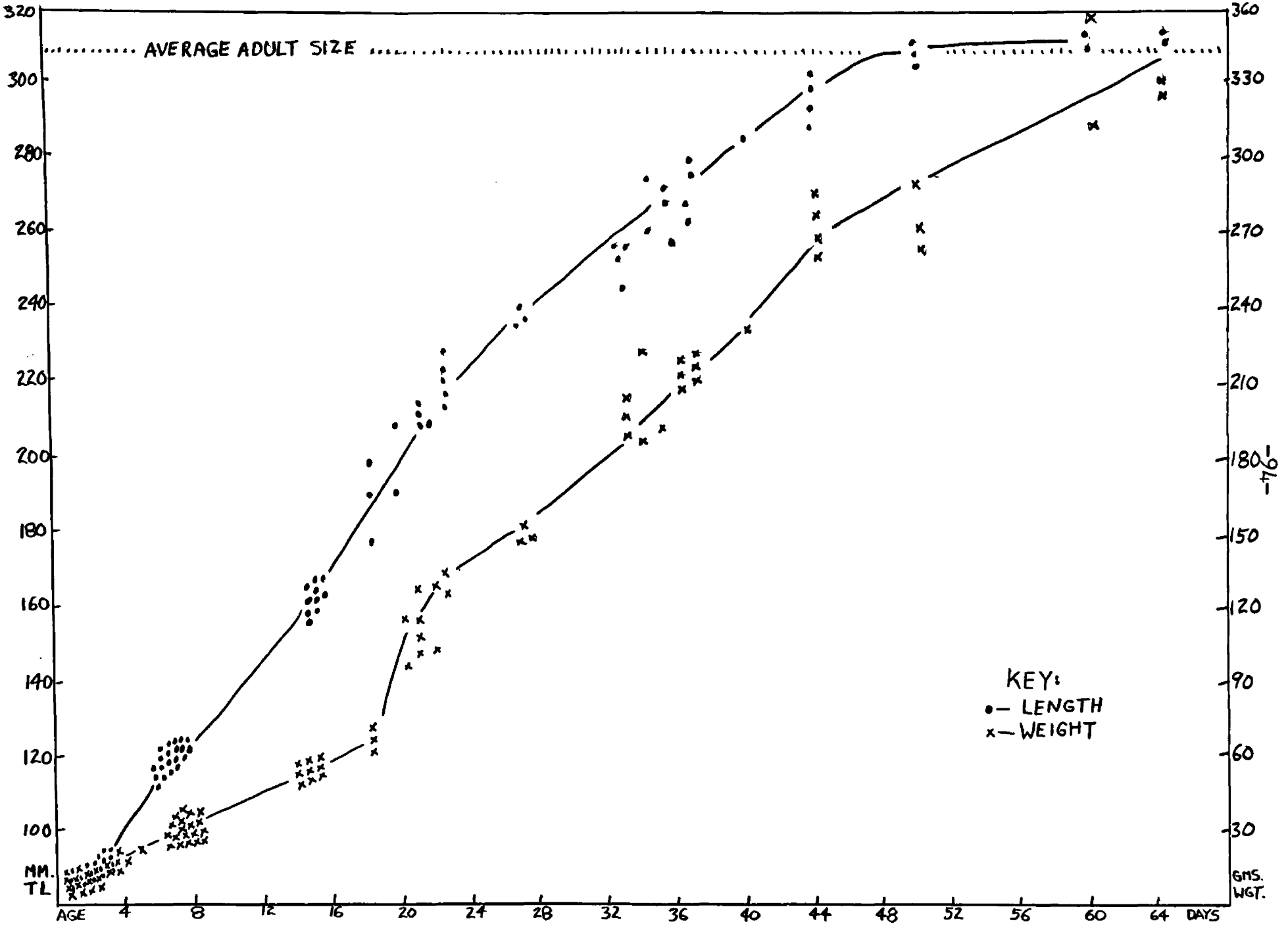

FIGURE 5. Total length and weight growth of ptarmigan chicks in 1959.

also quite rapid. Table XIII shows the development of plumages in young ptarmigan.

Seven juvenal primaries are budding from their sheaths on the first day after hatching and have reached a length permitting flight (about sixty millimeters) in the second week, when the chick is still partially covered by natal down. The finely mottled grey and brown juvenal plumage is complete in the third week and the dark inner primaries are beginning to be replaced. A white outer primary begins to show, which after comparing with Salomonson's (1939) work on Rock Ptarmigan, I conclude is the ninth primary and the first of the white first-winter primaries to appear. The outer two white primaries are slightly less white than the inner ones: white, grey, and cream color, respectively, from inside to out. By the end of the fourth week an inner white primary appears (presumably number one of the first winter plumage). These inner primaries appear in order approximately one every week thereafter. The dark juvenal primaries are molted faster so that a five week old bird may have only five or six primaries of three different appearances. Wing and tail feathers have approximately reached full length at the end of six weeks. The bone growth in the wing is nearly completed and the post-juvenal molt to autumn feathers is completed at the end of six weeks. One week later the molt to white winter plumage commences. Thus an eight-week-old chick may have three different kinds of feathers: a few juvenal, such as primary 8, considerable first fall plumage, and some white first winter feathers.

The juvenal and first-fall feathers have a lighter rachis and a softer texture than those of the adult. Probably the young can be distinguished from the adult even after they have attained the fully white

TABLE XIII. Development of the wing and certain plumages in young ptarmigan

Age Weeks	Wing Length in mm.	Tail Length in mm.	Primary Length in mm.	No. of Juvenal Primaries	No. of First Winter Primaries	Plumage Type
1	30-54	none-16	none-52	7	none	natal down
2	50-59	16-38	50-80	7 or 8	none	full juvenal primaries
3	57-67	38-58	75-100	about 6	#9 begins	full juvenal body
4	65-75	58-78	99-125	about 4	#1 begins	first white primaries
5	73-81	76-84	120-130	about 3	1, 9, 10	full fall plumage
6	80-85	82-90	130-137	about 2	1, 2, 9, 10	
7	83-88	84-97	135-140	about 1	1-4, 9, 10	begin winter molt
8	84-90	85-97	135-140	about 1	1-5, 9, 10	
9	85-92	85-97	135-140	none	1-6, 9, 10*	
completion of growth	7 wks.	6 wks.	6 wks.		* primaries 7 and 8 not yet appeared	

winter plumage or their first year nuptial plumage by the presence of the two slightly colored outer primaries. Sexes of the chicks could not be clearly determined although some difference was noted after about six weeks. Two sub-patterns of the first fall coat were observed. Some birds had a somewhat browner plumage, particularly on the breast. These were often somewhat smaller birds and were possibly females as differentiated from larger, grayer males. A corresponding difference occurs in the fall plumage of the adults at this same time.

Behavioral changes. During the first week the chicks hide from potential predators mostly by crouching beside a rock or similar object at the warning call of the hen. When suddenly frightened, the chicks run, often toward the hen. At this time, they usually can be hand-captured for observation because their speed is not great and they tire in a short time. However, strength for fast running and flight comes quite rapidly in the precocial development of these ptarmigan.

Chicks use their wings for lift, enabling faster running, by the fifth day and week-old chicks flap them considerably. By ten days, chicks can fly short distances and at the end of the second week can fly over twenty-five feet, making them very difficult to capture.

After the first week, a chick commonly runs and/or flies to a rocky area or even into krummholz rather than to the parent for protection. One two-week-old chick was observed to go into a ground squirrel hole to hide. This early self-reliance in hiding and escape actions is probably an important factor in the low apparent mortality rate of chicks (about one in three during the first eight weeks (see Page 25). This low figure suggests that most chick mortality takes place in the first week.

However, some loss may occur from chicks getting lost during such independent dispersal when danger threatens.

Particularly in the earlier portions of the growth period (two to three weeks old) chicks often begin crying for their mother in three to five minutes after dispersal. Since chicks often fly in all directions from their original group, a few of them have difficulty in relocating the hen. The constant clucking by the hen usually guides the chicks back. Two instances were observed in which the chick must not have heard this clucking and set out in the wrong direction to find the hen. The observer returned these lost chicks to their broods after they had been lost for thirty minutes and it was clear that they would not have returned by themselves except by chance. In the first case, a two-week-old chick was over one hundred feet from the hen (who went in the opposite direction at the time of disturbance) and could not hear her calls. In the second case, an older chick (about four weeks) had flown fifty feet down a stream to escape and could not hear the mother's calls over the sound of the water. Size variation of certain chicks in broods (e. g. chick 79, Table VIII) is probably due to the chick being from another brood. A lost chick would probably respond to the calls of another hen and join that brood.

A chick which had crouched beside a rock for camouflage could be approached more closely than a "hiding" parent bird, although there is sone individual variation. This hiding crouch tended to be held longer when the parent or another chick was also crouched nearby. A lone chick sometimes gave himself away much sooner than necessary for escape. The hiding tendency decreased as chicks became older, up to about six weeks, after which they were more likely to fly than adult birds.

The great diversity of foods taken by young chicks has been commented on above. As chicks became older, they fed on increasingly similar foods. This reduction in individual variation is probably a result of lessened experimentation with foods and increased learning and mimicking of the choices of the hen. Some individual variation persisted, indicating preferences for different foods.

Attainment of Full Body Size

Physical characteristics. Maturity of measured external body characters was complete by the end of the seventh week in all respects except weight which lagged about one week behind (see Tables VIII and IX and Figure 5). The first conspicuous winter body feathers appeared at seven weeks coincident with attainment of mature body form. Since primaries 9 and 10 are not quite as white as the others, young of the year could be distinguished throughout the study despite their similarity to adults in body size.

As the young ptarmigan attains maturity, it begins to make calls other than the loud cheeping of the chick and the juvenile bird. However, cheeping calls were heard as late as October from young (about eleven weeks old) that were still with their mother. Young which were independent were not observed to use this call. Instead they gave many calls which sounded identical to such adult calls as clucking, annoyance "churrs," and aerial-danger warning calls. There is considerable variation in pitch, but at maturity it generally approaches that of the adults.

Flight is strong and closely approaches that of adults once most of the first-year primaries are grown (e. g. at nine weeks when 1-7,

9 and 10 may be grown). Chicks above eight weeks of age were observed to fly distances over one hundred yards.

No differences in food choice were observed between adults and maturing young ptarmigan. The transition to the adult diet seems to be essentially complete by the end of six weeks of growth.

Behavioral changes. After eight weeks, chicks began to be observed alone. For a period of two weeks after this some chicks disappeared from the brood only to reappear after a few days. Other chicks were discovered temporarily with different broods or with independent chicks from broods other than their own. Variation in independence was observed in individual chicks, some leaving the brood considerably before others. Some chicks were seen with their parents at eleven weeks of age, but these were exceptional instances. About half the chicks observed were independent by the end of the ninth week.

Differences in independence were noted between broods. Some hens ignored their chicks once they became about nine weeks old. Correspondingly, these chicks left the hen somewhat before most of the chicks did.

A few chicks managed on their own and appeared adjusted to an independent state within a day or two of leaving the hen. However, many returned to the hen or to other ptarmigan on occasions during at least two weeks after initial independence. Others, as pointed out above, had not clearly become independent by the end of observation (their eleventh week). Therefore, I conclude that most young ptarmigan require some close contact with their parent or other ptarmigan for at least a few weeks after initial independence.

Attempting to maintain this close contact with other ptarmigan

caused many young birds apparent frustration. Many observations were made of young birds getting too close to strange adults and being aggressively driven away. Male birds were observed to drive chicks away with the most aggression and to respond at the greatest distances (up to four feet was observed), but strange females also hissed at and/or drove away young which ventured too near.

Young ptarmigan seemed to adapt themselves readily to the "responsibilities" of adulthood. In fact, young birds often were the most alert in a flock of ptarmigan and would be the first go give a warning call for an eagle flying in the distant sky or an approaching human. The young birds, after about ten weeks of age, also seemed to cope with weather effects such as strong winds and sleet at least as well as the adult birds.

SUMMARY AND CONCLUSIONS

1. The reproductive behavior of White-tailed Ptarmigan (Lagopus leucurus) was studied during the summer of 1959. Observations were made on a population of over one hundred individually marked ptarmigan residing at least part of the summer in an area of about three square miles near Logan Pass, Glacier National Park, Montana.

2. The study area lies astride the Continental Divide and is a glacially-leveled benchland covered with numerous small ledges. The highest relief and the surrounding mountain peaks lie primarily along the western boundary of the area. Prevailing westerly winds thus do not strike most of the area at maximum velocity and do not drop considerable moisture on the study area in passing over it.

3. Weather information was gathered at four stations on the study area with both continuously-recording and instantaneously-measuring instruments. Temperature, relative humidity, precipitation, wind velocity, and cloud cover were recorded. The phenological summer of 1959 at Logan Pass appears to have been shorter, cooler, and wetter than the previous summer. Four fairly distinct phases of weather were recorded during the study. Clear and mild weather in mid-June was followed by cool and wet weather in late June and early July. Five weeks of continuous warm, dry weather throughout the rest of July and early August was followed by cool and wet weather for the remainder of the study period. The abundance of moisture, and good weather during the first few weeks after hatching of chicks probably benefitted the ptarmigan population and counteracted the detrimental effect of the phenologically late season.

4. The Logan Pass study area lies within an ecotone between montaine tundra and taiga biomes. Within this ecotone eleven plant associations have been delineated: wet meadow, wet heath-sphagnum, Carex, willow, dry meadow, wet rock ledge, dry rock ledge, krummholz, heath mat, fell-field, and rock. Ptarmigan have been primarily observed in wet meadow, wet rock ledge, dry rock ledge, and fell-field associations. The latter two appear to be primarily used when the vegetation is young.

5. A total of 145 White-tailed Ptarmigan were banded during the study. Of these, sixty-eight were adults banded at Logan Pass. Observations and bandings of new birds continued throughout the season. An average of seven ptarmigan were seen per day. Changes in relative numbers of individuals in sex and age classes were recorded throughout the summer. The population of adult ptarmigan on the study area was determined by various methods to be between forty-nine and sixty individuals. Observed chick loss was twenty-three per cent in nine broods (32 chicks) over an average period of forty-seven days.

6. Territoriality was exhibited to at least some degree by most male ptarmigan. About twenty-five per cent of males occupied territories consistently throughout the early or territorial period of the summer, from mid-June to mid-July. A total of thirty-three areas were observed to be occupied by male ptarmigan for periods over one day. The average area occupied was 44 x 25 yards in size and usually was a rock ledge of some sort. Also characteristic of territories was abundant moisture and fresh vegation. The vegetation characteristic of the continually-occupied territories was a combination of wet and dry ledge associations interspersed with patches of heath and krummholz.

7. Continually occupied territories were all established before the beginning of July (the middle of the territorial period). Establishment apparently takes place on a first-come-first-served basis when a male who is visiting suitable areas finds one unoccupied. Some areas were maintained continuously (ten to forty-two days), others intermittently for periods (up to four days each) totaling up to fourteen days, and still others only temporarily for periods of from one to four days. On continually-occupied territories resident males were not observed to leave their areas throughout the middle of the territorial period. Paired birds in particular spent the entire day on a territory.

8. Defense of the territory was observed to be most intense when mating was taking place, about one week before the middle of the territorial period. Fighting was observed between males on a few territories, with the resident male appearing dominant in each case. The call of one cock excites retort from another male hearing it and apparently will elicit attack behavior from a resident male (on his territory). In every observed case, attack by the resident male resulted in the intruder taking wing and being pursued by the resident male. Defense was not observed to be directed toward anything but an intruding male ptarmigan. A decline in defensiveness after the middle of the territorial period was apparent, which is possibly correlated with plumage change and related testis size. No reoccupation of territory was observed, but an increase in calling by males in the fall was noted.

9. Mate selection seems to be primarily carried on by the female. Her selection may take place either early in the season during courtship flights, or later through visits to males on territories. The relative importance in pair formation of each of these two actions or a combination

of the two was not determined. The reasons for selecting a particular male as a mate by a female were not clearly discerned. Selected males appeared dominant and occupied territories apparently containing the most "preferred" habitat. These males may have been nearest the peak of breeding condition, or merely the first to occupy "preferred" territories.

10. The pair bond, when established, appears quite strong. In most cases the two birds were rarely observed over fifteen feet apart throughout periods of over ten days. Paired males defended not only the territory but also the female from enemies. Such males would make themselves conspicuous first when the pair was approached and frequently would keep between the intruder and the female of the pair. Pairing ended when the female either left the territory, was killed, or began incubating eggs. Some re-pairing was observed. Some promiscuity was observed and probably occurs occasionally even among paired birds.

11. A number of mating displays were observed. A scream-like courtship call and two mating calls are described. Two kinds of special flight patterns were observed. One of these is a crepuscular pursuit flight in which both male and female or two males were observed to participate. The role of this flight in courtship, dominance, or both was not clearly determined. The second flight was observed only once. It consisted of a spiralling, vertical flight performed over the territory by the male of a pair. This flight appears similar to a courtship flight observed in Rock Ptarmigan (L. mutus). A strutting display performed by the male immediately prior to copulation is described. This display is somewhat complex, but is basically similar to the strutting displays of other grouse. Copulation is described; it is brief and often repeated

during a period of sexual excitement. Following one sequence of several copulations a special post-copulation activity was observed in which the male repeatedly seized objects and dropped them on his back and to the side of his tail.

12. Three nests were found during the study. These suggest that a small nest territory is established by the hen. Characteristics of the site include nearness to rocks, water source, and superior food sources. Nests also are inconspicuous by color, cover, or both, and are generally protected from flooding and excesses of sun and wind. Nest sites appear to be chosen by the female through visiting suitable areas both on and off the male's territory. Selection appears to be made immediately prior to laying the first egg. Moist, phenologically young sites were chosen in each case. Nest construction varied greatly and no pattern was determined. The male takes little or no interest in the nest.

13. Laying interval between successive eggs was approximately thirty hours with considerable variation and apparently with a longer interval before the last egg. Laying took place at all hours of the day. Laying behavior was observed once. The process took about forty-five minutes and included several copulations by the attendant male. Clutch size averaged 5.2 eggs. One large clutch may have been contributed to by two females. Eggs were measured and are described.

14. In the two observed cases, incubation began before the last egg was laid. Incubation lasted just under twenty-four days in the one recorded case. Hens were almost never observed off the nest during the entire incubation period. Some weight loss in incubating hens is indicated. After about the third day of incubation, hens refused to leave the nest even when considerably disturbed, and associated mild defensive

reactions were observed. Overheating during warm weather may be more detrimental to incubating hens than effects from inclement weather. Incubating females exhibited large brood patches. Males appeared to take no part in incubation or care of the young.

15. Hatching took place at nearly the same time for six of the nine eggs of one clutch. Because of the precocial nature of ptarmigan chicks, eggs must hatch at nearly the same time for all chicks to survive. The hatching period in 1959 was between July 16 and 25 for all ptarmigan broods observed. The hatching process took about two days from the first audible pipping to emergence from the egg. The hatching process includes not only pipping a hole in the egg, but lateral chipping with the beak and twisting and straightening actions of the whole chick's body. The hen led the newborn chicks away from the nest within about eight hours of the time they emerged from the shell. Unhatched eggs and shell remains are left in the nest.

16. Twelve broods with an average of four chicks each were observed. Measurements of chicks were taken from hatching until attainment of full body size. Total length showed a rapid, linear growth to full size in about six and one-half weeks. Weight increase appeared more sigmoid, lagging behind length in rate for the first two weeks. Adult weight is reached after eight weeks. Plumage change is very rapid in young ptarmigan. Seven juvenal primaries are budding when the chicks hatch. These grow rapidly enough to enable flight after the first week. Natal down is exchanged fully for juvenal plumage within two weeks. Post-juvenal molt is complete at the end of six weeks. One week later the moult to white winter plumage commences. This rapid growth appears to be a distinct advantage to the ptarmigan. Even in a phenologically

late year such as 1959 the young attain full size and are molting to white plumage before winter.

17. A hen-chick bond appears to be established even before hatching, and is formed by the peeping of the chicks from within the shell and the subsequent response call of the female. Day-old chicks fed on a variety of foods. These foods are taken experimentally and at the example of the hen who occasionally gives an assembly call when she discovers a good source of food. Feeding and brooding intervals of day-old chicks were both about twenty minutes long. Brooding lessened and resting by the chicks on their own increased after the first day. The last observed brooding was of ten-day-old chicks which had just begun to fly well. Chicks relied on the hen for danger warnings during the first two weeks but rapidly became alert to dangers thereafter. "Freezing" and hiding actions were observed from the first day onward. Self-reliance in escape and hiding behavior was shown by chicks over two weeks old. A radial dispersal pattern when disturbed often results from this self-reliance which may produce lost chicks. Calling of a lost chick and response by the hen serves to reunite the brood in most cases. However, mortality or joining of another brood by the chick appears to result in some cases.

18. Two forms of defense of the chicks by the hen were determined. An aggressive defense including both threat-display and attack was shown by hens in response to distress calls from chicks. A non-aggressive defense was noted, consisting of warning the young and a distraction display which served to hide the chicks and lead the "enemy" away. This non-aggressive defense appears to be released by sight of danger or threat to the chicks rather than the chicks' calls. Intensity of defense varied with the amount of familiarity the hen had with the "enemy" and

the completeness of the brood. Hens generally could not recognize the size of their brood.

19. Chicks began to leave the brood after eight weeks, but some were still with the hen after eleven weeks. Most young ptarmigan appear to require some close contact with their parent or other ptarmigan for at least a few weeks after initial independence. Intolerance of juvenile birds by many adult ptarmigan was observed. Some males clearly showed aggressiveness when young approached them too closely.

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APPENDIX

Photographic Plates

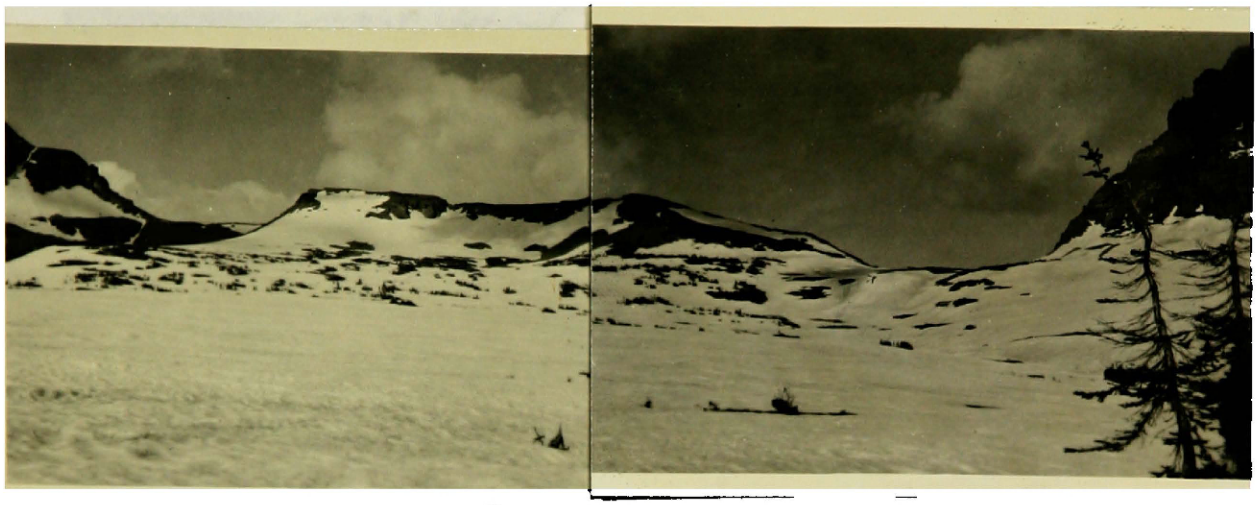


PLATE 1. View of study area toward Grizzly Mountain (center) and Hidden Lake Pass (right) July 2, 1959.

PLATE 2. View across Oberlin cirque to Reynolds Mountain, July 2, 1959. The ledge just left of center in the cirque is ptarmigan territory number one.

PLATE 3. Male (left) and female (right) ptarmigan paired on territory 7, June 25, 1959.

PLATE 4. Male ptarmigan guarding mate on nest (circle) while she lays an egg, July 9, 1959.

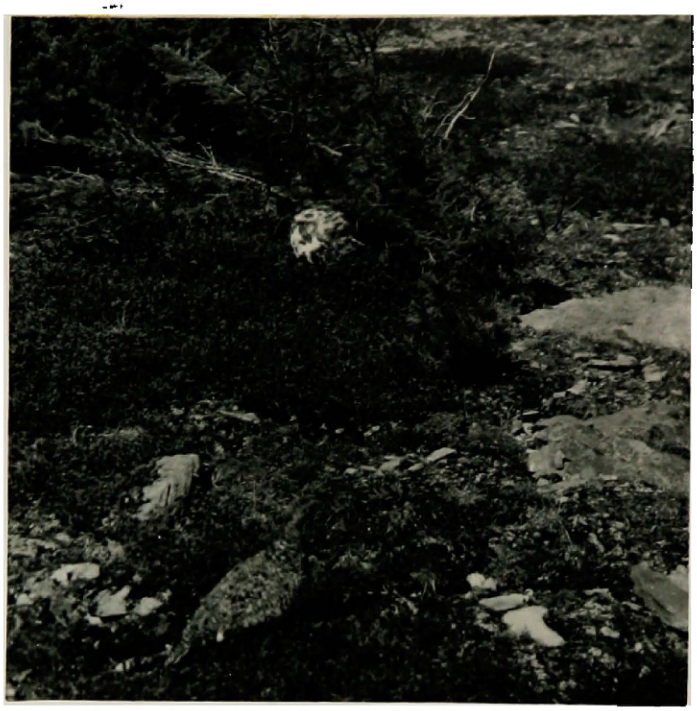
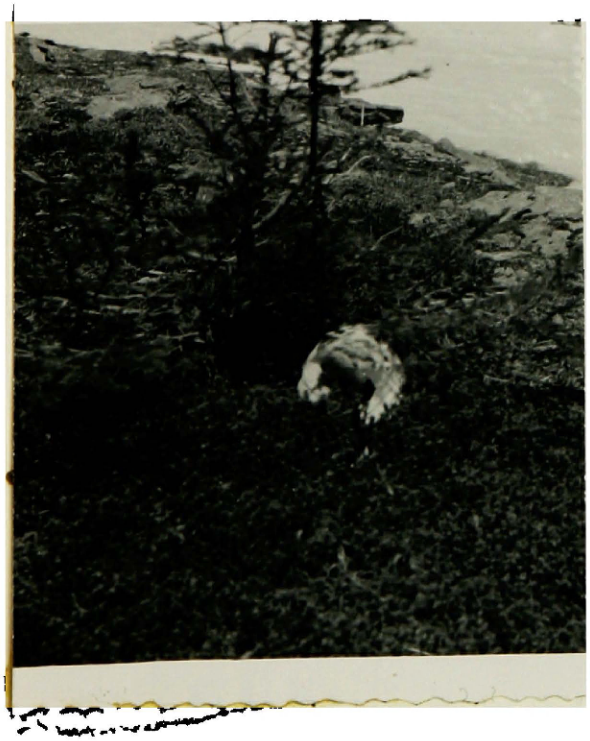


PLATE 5. Male copulating with female on the nest in full view of "intruding" female, July 1, 1959.



PLATES 6,7. Male copulating with his mate on the nest (left), and copulating with the intruding female (right).

PLATE 8. The same male chases the intruding female away from the nest where his mate is laying and egg (circled). Plates 5-9 taken from 1-2 p.m. on July 1, 1959.

PLATE 9. The laying female driving the intruding female away from the nest without leaving the eggs, July 1, 1959..

PLATE 10. Ptarmigan nest after hatching showing abandoned shell remains, July 26, 1959.

PLATE 11. Ptarmigan hen with chicks under four days old. Four (circled) chicks visible. July 26, 1959.

PLATE 12. Half grown chick, illustrating crouching and hiding action behind a rock. August 17, 1959.

PLATE 13. Hen (right) and nearly grown chick, August 30, 1959. Note plumage difference and rigid, "freezing" of chick even when in plain sight.

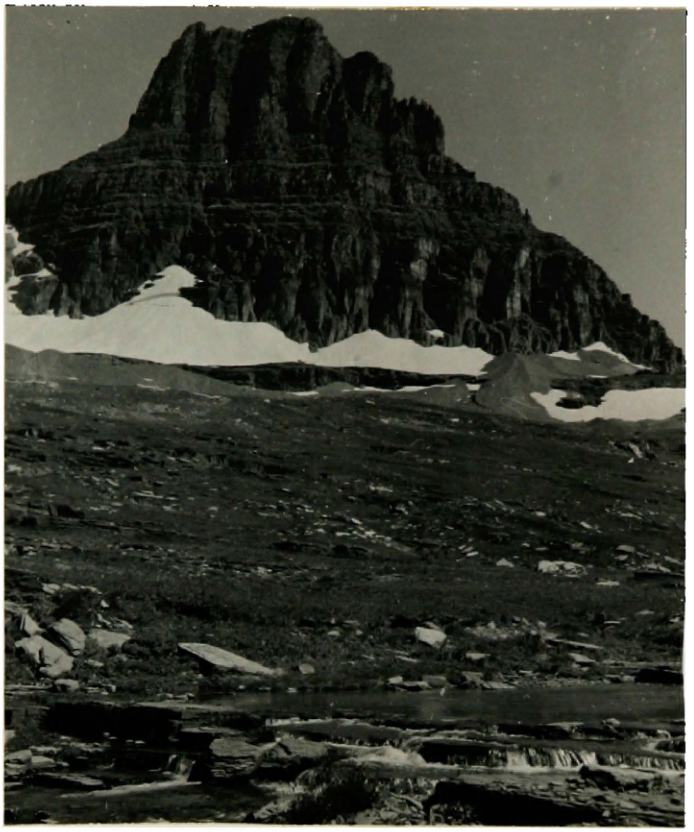


PLATE 14. Late summer habitat view, looking from Reynolds Creek to Mount Clements, August 30, 1959.

PLATE 15. Full-grown chick on September 22, 1959, showing molt from dark fall to white winter plumage.